USDA FOREST SERVICE GENERAL TECHNICAL REPORT PNW-65
1978

CASE HISTORY of an Excellent White Spruce Cone and Seed Crop in Interior Alaska:

Cone and Seed Production, Germination, and Seedling Survival

By
John C. Zasada
M. Joan Foote
Frederick J. Deneke
Robert H. Parkerson

Pacific Northwest Forest and Range Experiment Station
Forest Service U. S. Department of Agriculture
Portland, Oregon

ABSTRACT

Excellent cone and seed years are important for both natural and artificial regeneration. The 1970 white spruce (*Picea glauca* (Moench) Voss) cone and seed crop was the best crop produced by this species since 1958 in interior Alaska. The crop provided an opportunity to make detailed observations of growth and development of cones and seeds, seed dispersal, seed germination, and seedling establishment.

Flowering at lower elevations (135 meters) occurred in late May; but above 600 meters, it occurred 3-5 weeks later. Growth of cones in physical dimensions was essentially completed by early July; however, dry weight increased through August. At 135 meters, seed maturity increased from early July to early August with little change in physical appearance of the endosperm and embryo, and real germination increased from early August to seed fall. Poorly developed seeds (i.e., immature embryos) were observed in collections above 600 meters and north of the Arctic Circle. Seed dispersal at 135 meters occurred 99 days after peak pollination. Total seed fall in undisturbed white spruce stands varied from 250 to 2,000 seeds per square meter; filled seed varied from 38 to 77 percent of total seed fall.

Germination of this seed crop at a study site near Fairbanks began in late May 1971 and exhibited two distinct peaks in activity which were associated with high soil moisture in early summer and midsummer. White spruce seedling mortality was greatest during the first winter when survival was reduced from about 90 to 30 percent. By the end of the fifth growing season, mortality had reduced survival an additional 10 percent. Comparative germination and seedling establishment data are presented for paper birch (*Betula papyrifera* Marsh.).

KEYWORDS: Cone production, seed production, seed crops, seed dispersion, seed quality, regeneration (natural), natural regeneration, regeneration (artificial), artificial regeneration, population dynamics, white spruce, *Picea glauca*, paper birch, *Betula papyrifera*, Alaska (interior), interior Alaska.

JOHN C. ZASADA and M. JOAN FOOTE are research forester and general biologist with the Pacific Northwest Forest and Range Experiment Station.

FREDERICK J. DENEKE was a forester with the U.S. Army Cold Regions Research and Engineering Laboratory, Fairbanks, Alaska, at the time of this research. He is now a geneticist with Cooperative Forestry and Fire Protection, State and Private Forestry, Rocky Mountain Region, USDA Forest Service, Denver, Colorado.

ROBERT H. PARKERSON was a research associate with College of Renewable Resources and Agricultural Sciences, University of Alaska, Fairbanks. He is now manager of the Alaska Plant Materials Center, Palmer, Alaska.

ACKNOWLEDGMENTS

Donald Lovig assisted in all aspects of this study and deserves special thanks. The Bureau of Land Management, U.S. Department of the Interior, assisted in the collection of seed from areas away from the road system and provided financial assistance. The Alaska Department of Natural Resources, Division of Lands, assisted by clearing the area used for seedling survival observations. The late Professor Risto Sarvas of the Finnish Forest Research Institute contributed significantly to the design of this study through his publications and our correspondence with him.

CONTENTS

ENGLISH EQUIVALENTS

(9/5°C) + 32 = °F

1 centimeter = 0.39 inch

1 hectare = 2.47 acres

1 kilometer = 0.62 mile

1 square meter = 10.76 square feet

Introduction

Excellent seed years are important for success of both natural and artificial regeneration programs. At northern latitudes these excellent years occur at greater intervals than in southern portions of a species range (Sarvas 1957, Andersson 1965, Waldron 1965, Zasada and Viereck 1970, Chalupka and Giertych 1973). Thus, the occurrence of good cone and seed crops in the north is especially significant as they must provide the majority of seed for reforestation.

Records indicated that the 1970 white spruce (*Picea glauca* (Moench) Voss) cone and seed crop in Alaska was the most productive since 1958 (Zasada and Viereck 1970). From 1970 through 1975, relatively detailed observations were made of cone growth and development, seed maturation and dispersal, seed germination, and seedling establishment in order to assess the regeneration potential of white spruce under subarctic conditions. Cone and seed production were observed in 29 stands in Alaska and a transect along the Richardson Highway (fig. 1, table 1). These observations expand on certain aspects of a more general discussion of white spruce seed production by Nienstaedt and Teich (1972) and provide comparative data for northern white spruce genotypes. Seedlings were observed for the first five growing seasons, generally considered the period of seedling establishment, in a small forest opening located on the Bonanza Creek Experimental Forest near Fairbanks, Alaska.

This study is by no means definitive because annual variation in weather conditions, vitally important to successful regeneration, are not considered. The study was, however, an attempt to provide a relatively detailed case history of the stand establishment phase of white spruce management. We hope this research will help land managers achieve their management objectives and will give forest biologists added insight into the reproductive biology of a species near the northern limits of its range.

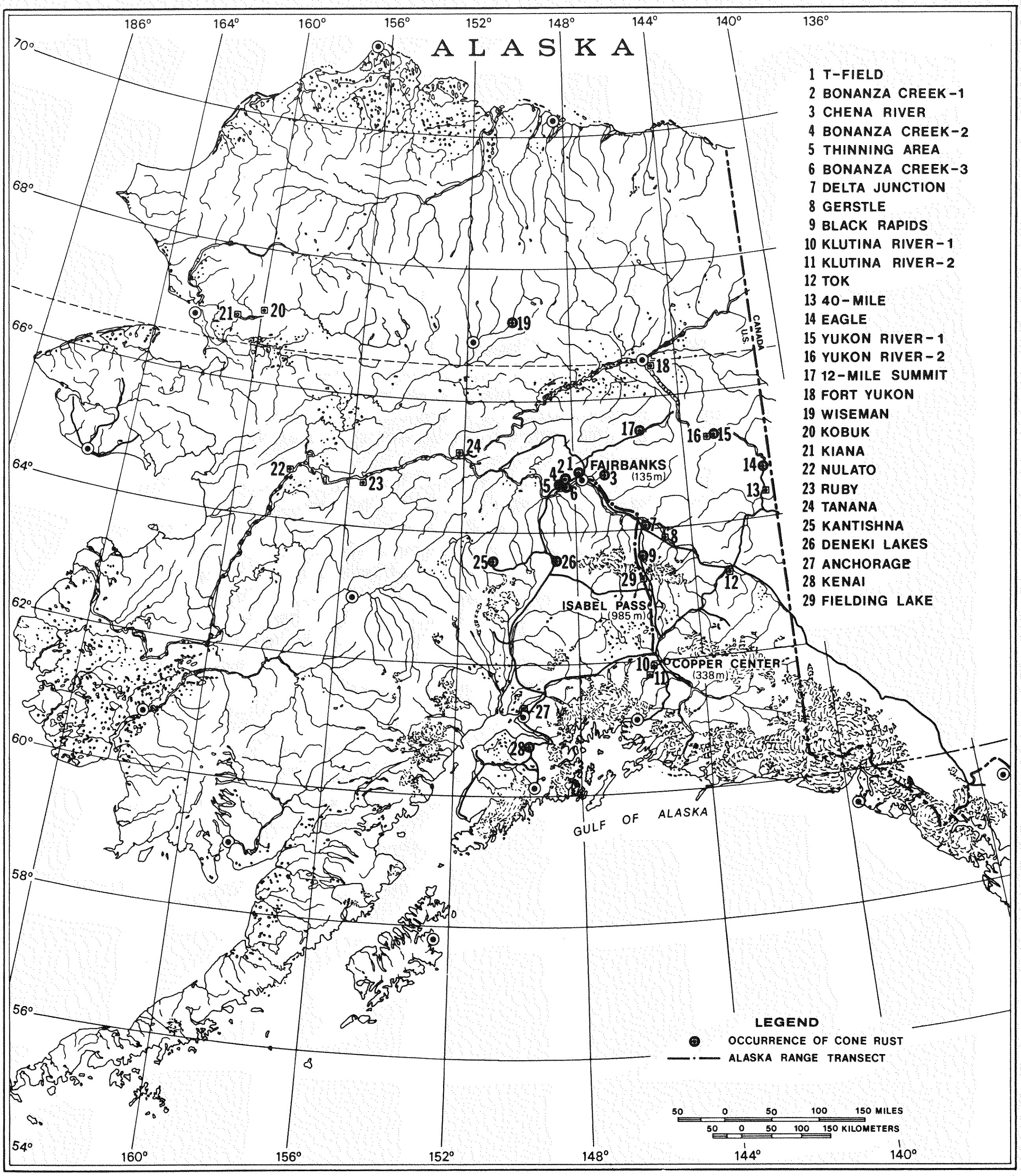


Figure 1.--Location of stands (▣) from which cones and seeds were collected from white spruce in Alaska in 1970.

Table 1--*Latitude, longitude, and elevation of white spruce stands in Alaska from which cones were collected in 1970--and cone length*

Stand number	Area	Latitude	Longitude	Elevation	Observation[1/]	Cone length (mm)	
						$\overline{X}$	Standard error
				Meters			
1	T-field	64°52'	147°50'	170	cd, t, c	40	1.2
2	Bonanza Creek-1	64°45'	148°20'	385	t, c	34	.9
3	Chena River	64°53'	146°43'	200	t, c	36	1.1
4	Bonanza Creek-2	64°44'	148°20'	246	t, c	38	1.3
5	Thinning Area	64°44'	148°20'	230	t, c	36	1.0
6	Bonanza Creek-3	64°44'	148°05'	130	t, c	33	.8
7	Delta Junction	64°10'	145°50'	308	c	33	1.3
8	Gerstle River	63°55'	144°55'	370	c	31	1.0
9	Black Rapids	63°30'	145°50'	708	c	32	1.6
10	Klutina River-1	61°49'	145°32'	492	t, c	32	1.3
11	Klutina River-2	61°53'	145°33'	570	t, c	40	2.5
12	Tok	63°10'	143°10'	615	c	43	1.1
13	40-mile	64°26'	141°21'	523	c	38	1.4
14	Eagle	64°46'	141°12'	338	c	38	1.2
15	Yukon River-1	65°20'	143°05'	215	t, c	39	1.3
16	Yukon River-2	65°20'	143°05'	215	t, c	40	1.4
17	12-mile Summit	65°20'	146°05'	769	c	36	2.2
18	Fort Yukon	66°35'	145°18'	129	c	37	1.1
19	Wiseman	67°25'	150°05'	492	c	37	1.2
20	Kobuk	66°52'	156°50'	46	c	40	1.7
21	Kiana	66°44'	160°25'	30	c	38	1.0
22	Nulato	64°44'	158°05'	33	c	38	1.2
23	Ruby	64°45'	155°30'	62	c	32	2.1
24	Tanana	65°10'	152°05'	65	c	29	1.7
25	Kantishna	63°31'	150°54'	615	c	35	2.0
26	Deneki Lakes	63°37'	148°42'	660	c	37	2.0
27	Anchorage	61°10'	149°40'	69	c	39	1.2
28	Kenai	60°20'	149°30'	308	c	50	1.3
29	Fielding Lake	63°10'	145°35'	892	c	28	.8

[1/] cd = cone development; c = cone collection; t = seed traps and cone counts.

Cone and Seed Production

MALE STROBILI DEVELOPMENT

Methods

Development of male strobili was observed on three trees in stand 1, T-field (fig. 1). Collections were made at 1- to 3-day intervals from May 15 to 27. A final collection was made on June 3 after all pollen had been dispersed. On all collection dates except May 25, 20 strobili were collected from each tree. On May 25, obvious external differences existed between strobili on the same tree, and 20 collections were made from each of the following categories: (1) no open pollen sacs, (2) 50 percent or less of pollen sacs open, and (3) more than 50 percent of pollen sacs open.

Collections were made between 0600 and 0700 hours, placed in plastic bags, brought to the laboratory, and weighed within 1 hour of collection. Pollen loss appeared minimal. Drying was at 65°C for 24 hours.

Pollen density and seasonal periodicity were measured with one recording pollen sampler (Sarvas 1968) in stand 1, T-field (15 m above ground) and two each in stands 2 (Bonanza Creek-1) and 3 (Chena River), 30 m above ground. These heights corresponded with the base of the female cone-producing portion of the trees. Samplers were changed weekly.

Results and Discussion

The first sign of bud expansion was observed several days before collection of the first sample on May 15. By May 15 all male buds were noticeably expanded, and the apical portion of some strobili was visible. Dry weight of the male buds for the three trees ranged from 0.017 to 0.019 gram, and moisture content varied from 322 to 366 percent of dry weight (fig. 2). Increases in dry weight between May 15 and 21 were between 110 percent (tree 1) and 190 percent (tree 3) and moisture content between 190 and 260 percent.

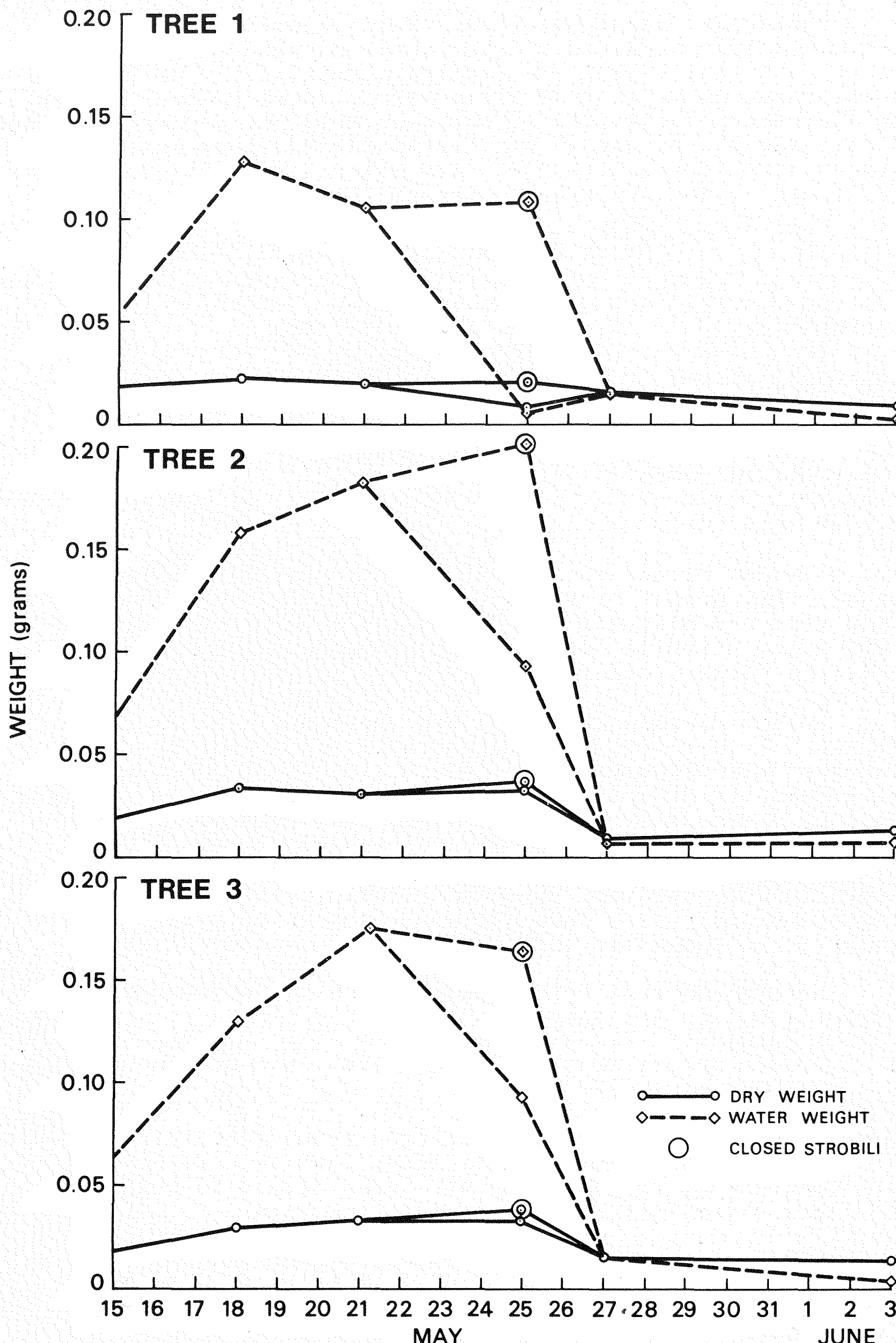


Figure 2.--Seasonal changes in dry weight and water weight of male strobili of white spruce.

Pollen dispersal was first observed on May 22, although maximum dispersal did not occur until May 25. The male cones on an individual tree varied significantly in stage of development on May 25. Differences in developmental stages on the basis of external appearance could not be distinguished before May 25; on May 25 at least three developmental stages were distinguishable. Dry weight and moisture content for these stages for tree 1 were as follows:

	Dry weight (Grams)	Moisture content (Percent)
Unopened	0.02	550
Partially opened (50 percent or less unopened pollen sacs)	.02	200
Fully opened (more than 50 percent of pollen sacs open)	.01	58

The majority of the pollen was shed by May 27 in these three trees. Dry weight of strobili on May 27 varied from 0.01 to 0.02 gram and moisture content from 67 to 102 percent. By June 3 the strobili contained essentially no pollen and moisture content was less than 50 percent.

Pollen dispersal, as measured by the pollen samplers, in stand 1 (T-field) agreed reasonably well with the observations of the developing male strobili through May 27. Only small amounts of pollen were observed on the samplers before May 24. Large quantities of pollen were dispersed from the sample trees on May 25 and 26, coinciding with a large accumulation of pollen on the sampler. From May 28 until about June 6, however, there was little relationship between the amount of pollen remaining in cones on the three sample trees and the quantity of pollen on the sampler (fig. 3).

Several factors contributed to the difference between strobili pollen and sampler pollen:

1. Pollen deposited on branches, needles, and other objects was redistributed by wind.

2. We observed on May 27 that some trees contained numerous unopened male cones, indicating that an undetermined percentage of the trees were less developed than the three sample trees and shed pollen later.

3. Large numbers of black spruce (*Picea mariana* (Mill.) B.S.P.) are within 200 meters of stand 1(T-field). On June 2 we observed black spruce dispersing pollen. The high pollen densities of black spruce which occurred in June probably contributed to pollen counts.

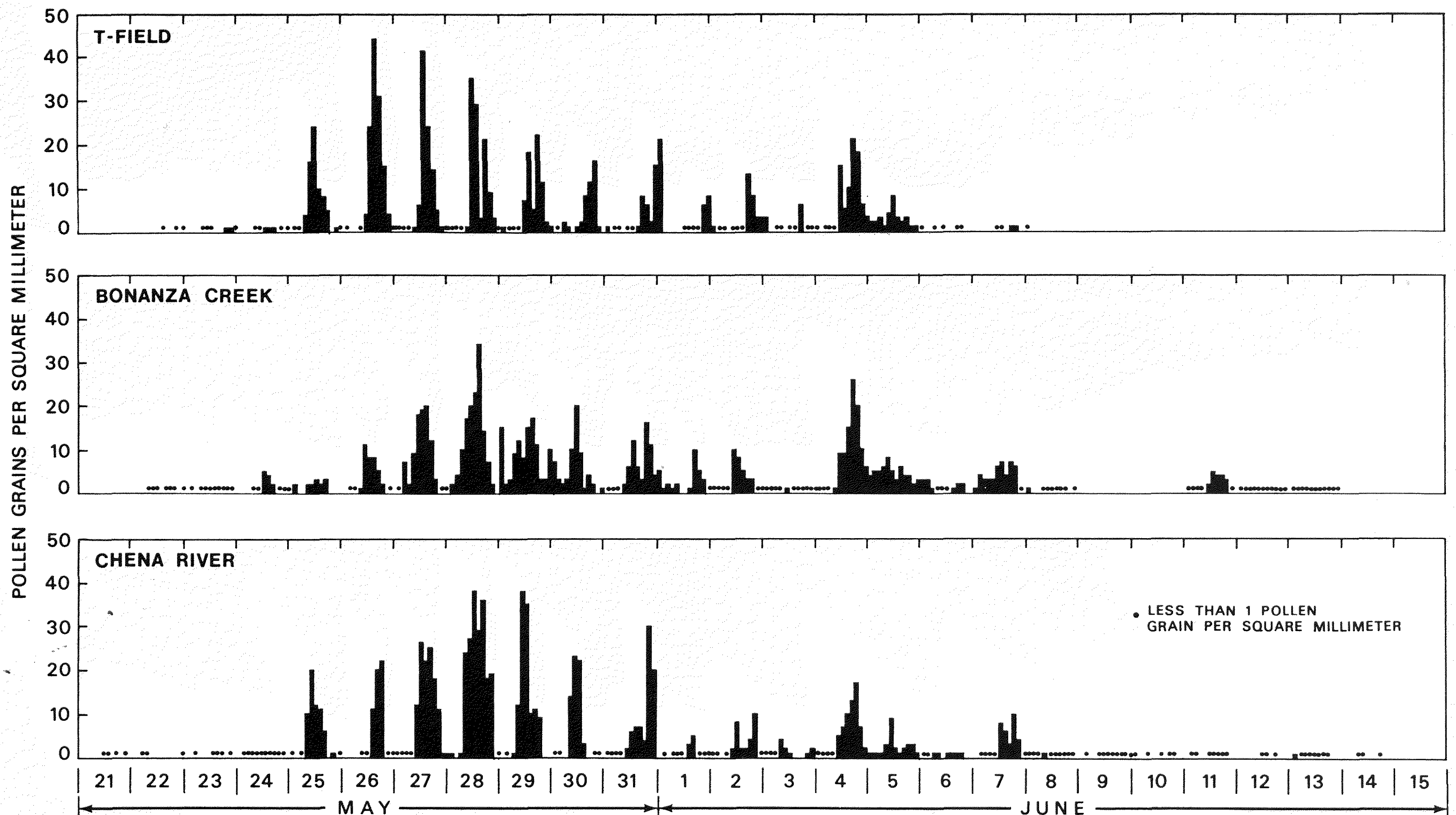


Figure 3.--Seasonal and diurnal course of pollen dispersal in three white spruce stands in Alaska.

4. In other white spruce stands in the vicinity--for example, stands 2 and 3 (Bonanza Creek-1 and Chena River)--peak dispersal did not occur until after May 27, about 2 days after large quantities of pollen were measured in stand 1, T-field (fig. 3).

The following tabulation shows the total amount of spruce pollen collected in each stand while the samplers were in place and while the female cones were receptive;

Stand number and area	Pollination	Pollen grains per square millimeter: During period of pollination	Pollen grains per square millimeter: Total (through June 15)
1, T-field	May 25 to May 30	510	690
2, Bonanza Creek-1	May 25 to May 30	668	824
3, Chena River	May 26 to June 1	513	741

Winton (1964) reported that anthesis varied from about May 12 to June 1 for white spruce in north-central Minnesota (about 48°N. latitude). Pollen dispersal in the vicinity of Fairbanks has not been observed earlier than mid-May nor later than June 10 (Zasada and Gregory 1969).

Additional observations of variation in timing of pollen dispersal were made along the Richardson Highway on June 26, 1970. This transect started at Fairbanks (elevation, 135 m) and passed through Isabel Pass in the Alaska Range (elevation, 985 m) to Copper Center (elevation, 338 m) (fig. 1).

Pollen dispersal was completed at both ends of the transect. At the lowest elevation (Fairbanks), however, development of female cones was more advanced than at Copper Center. At about 615 m, some pollen still remained in the male cones. At 770-920 m, pollen dispersal was commencing. In the scattered trees above 920 m, reproductive buds were just beginning to break (fig. 4). Male cone development at elevations of approximately 600 m or more in the Alaska Range appeared to be 3 to 5 weeks behind that in the Fairbanks area.

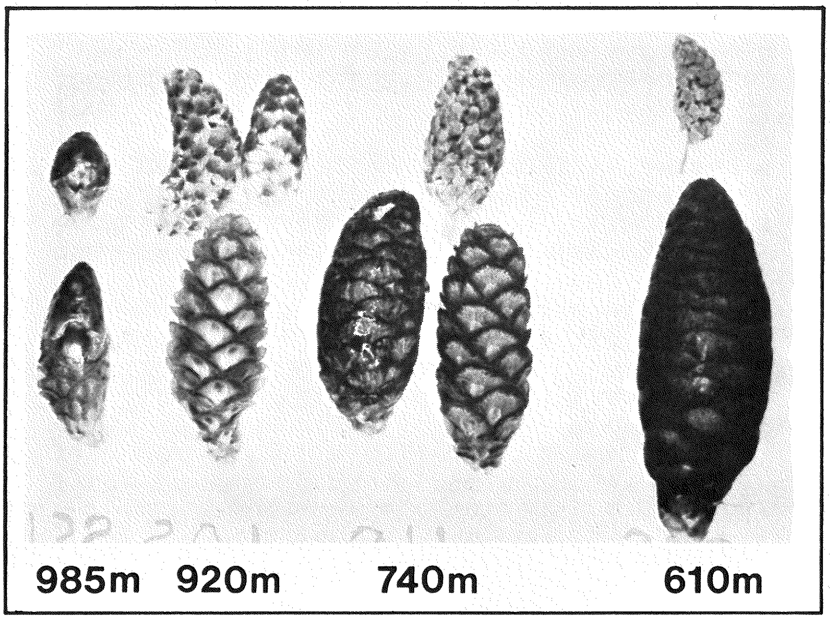


Figure 4.--Variation in male and female cone development on a transect made through the Alaska Range on June 26, 1970.

Strong diurnal patterns of pollen dispersal were observed (fig. 3). The general pattern was characterized by the dispersal of large amounts of pollen between 1000 and 1600 hours. Pollen dispersal was at a minimum between 2000 hours one day and 0400 hours the next day. This dispersal follows the humidity-temperature pattern; that is, peak dispersal at times of highest temperature and low humidity, and minimum dispersal at low temperature and high humidity. Exceptions to this general rule are common and are probably related to the occurrence of rain showers or to delays in normal daily warming.

FEMALE CONE DEVELOPMENT

White spruce cones are initiated the year prior to seed formation (Eis 1967a). Two factors frequently reported as important for reproductive bud formation are the climatic conditions at the time of differentiation and the cone crops of preceding years.

The climatic factors most closely associated with differentiation of large numbers of reproductive buds are above average temperatures and below normal precipitation (Fraser 1958, Matthews 1963). The temperature and precipitation during June 1969 fulfilled these requirements (table 2). Average daily maximum temperatures for four, 5-day periods beginning June 11 were 7°C above normal; minimum temperatures were 2°C above normal. Precipitation for June was 70 percent

Table 2--*Average maximum and minimum temperatures and precipitation for 1946-61,*[1/] *1969, and 1970*

Month and days	Maximum temperature			Minimum temperature			Precipitation		
	1946-61	1969	1970	1946-61	1969	1970	1946-61	1969	1970
	°C						Centimeters		
May:									
1-5	11.1	14.4	10.7	-2.2	-4.5	-2.6	0.03	0	0.05
6-10	13.9	14.7	15.9	-.6	2.0	1.2	.06	.09	.06
11-15	14.4	12.0	19.3	0	.4	1.6	.08	.40	0
16-20	17.9	18.5	18.6	2.2	2.7	1.0	.12	0	0
21-25	18.3	22.7	20.0	3.9	5.0	4.9	.20	.03	.88
26-31	18.9	17.6	20.0	4.4	1.7	3.6	.32	0	.42
June:									
1-5	21.1	19.7	20.1	5.0	2.5	2.8	.30	.36	.18
6-10	22.8	23.7	18.8	7.2	8.1	.9	.33	0	.14
11-15	21.1	29.0	18.2	6.7	10.9	5.4	.86	0	.14
16-20	22.8	29.4	21.0	7.8	9.2	5.9	.56	0	.06
21-25	21.1	30.6	22.1	7.8	10.5	7.3	1.19	0	1.21
26-30	22.2	28.0	20.7	8.3	9.1	8.2	.86	.50	1.02
July:									
1-5	22.2	22.2	23.8	8.3	8.9	10.9	1.22	.30	.12
6-10	22.8	22.8	20.7	8.3	10.0	7.4	.46	.15	.24
11-15	24.4	24.4	21.2	8.9	11.1	8.1	.76	.20	.15
16-20	22.8	22.8	20.0	9.4	10.0	8.8	1.14	2.56	.49
21-25	22.8	17.2	25.0	8.3	8.5	9.2	1.47	.99	0
26-31	15.0	14.4	23.5	8.9	6.1	9.5	1.30	.58	.24
August:									
1-5	20.0	19.4	18.6	7.2	10.3	8.0	.66	1.25	.60
6-10	21.1	12.1	19.2	7.2	1.7	5.7	1.07	.95	.32
11-15	15.0	13.7	22.2	7.2	-1.6	9.6	.74	0	.10
16-20	20.0	16.2	19.9	6.1	.9	7.1	.53	.03	.01
21-25	18.3	17.1	15.4	5.6	1.3	5.3	1.32	.27	.38
26-31	16.7	18.3	19.2	4.4	3.0	6.3	1.24	.02	.77

[1/] Funsch (1964).

below the average for 1946-61 (Funsch 1964). Average maximum temperatures for July 1969 were equal to or lower than the long-term average; minimum temperatures were both higher and lower.

Cone crops from 1967 to 1969 varied from failures to good crops. The last excellent cone crop and seed year occurred in 1958 (Zasada and Viereck 1970). The 1969 cone crop was fair to good in some stands and a near failure in others. A frost in late May 1969 caused 50-percent or more cone mortality above elevations of about 200 m in the area immediately adjacent to Fairbanks (Zasada 1971).

In summary, the history of cone crops of preceding years and the climatic conditions in the early summer of 1969 met criteria believed optimum for differentiation of a large number of reproductive buds.

Methods

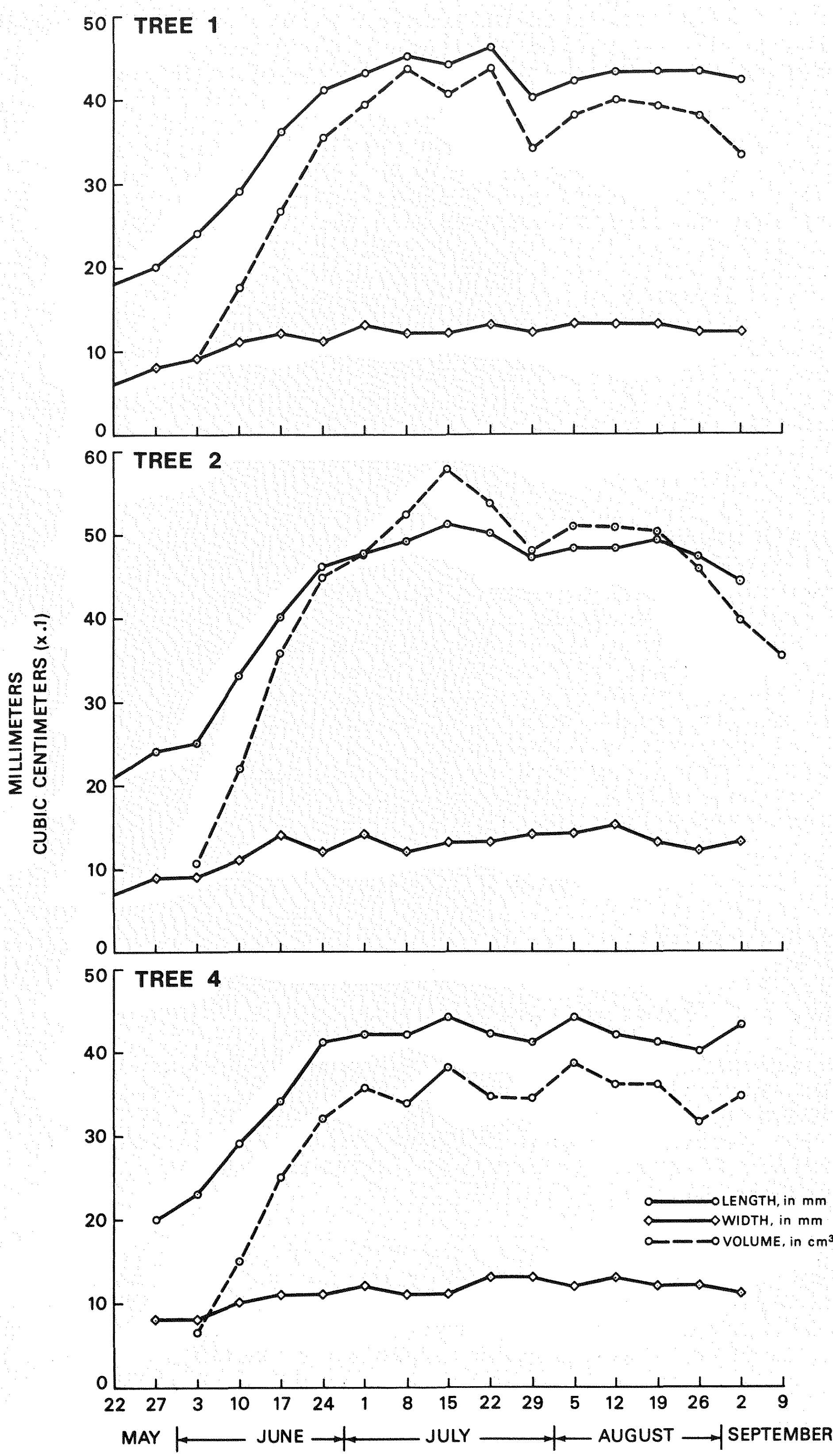
Female cones were collected from five dominant trees in stand 1, T-field, at weekly intervals from bud break until after seed fall began in September. These trees were growing in the same stand as those used in an earlier study (Zasada 1973). Sixteen cones were collected in each sample until July 8, and 30 cones thereafter. Trees were climbed, and each sample consisted of cones collected from different portions of the crown. Cone length was measured and volume determined by water displacement within 1-2 hours after collection. The cones were dried at 65°C until weight change was negligible. Dry weight was determined after cones were cooled in a desiccator.

Results and Discussion

By May 22, female cones were similar to those shown in the least developed cones in figure 4. All cones were fully exposed and cone scales fully opened by May 27. Scales on all cones had closed by June 1.

Growth of cones in physical dimensions (length, width, and volume) occurred primarily before July 1. Increases in cone volume were about 450 to 600 percent of initial values; 200 to 250 percent for cone length; 130 to 200 percent for cone width. Cone volume decreased slightly during the last four sampling periods (fig. 5).

The collection of cones from different areas of the State for the seed quality study provided an opportunity to examine variation in cone length over a large part of Alaska (table 1). Average cone length for these 29 stands varied from 28 to 50 mm. The largest cones were collected on the


TREE 1
TREE 2
TREE 4
MILLIMETERS
CUBIC CENTIMETERS (x.1)
50
40
30
20
10
0
60
LENGTH, in mm
WIDTH, in mm
VOLUME, in cm³
22
27
3
10
17
24
1
8
15
22
29
5
12
19
26
2
9
MAY
JUNE
JULY
AUGUST
SEPTEMBER

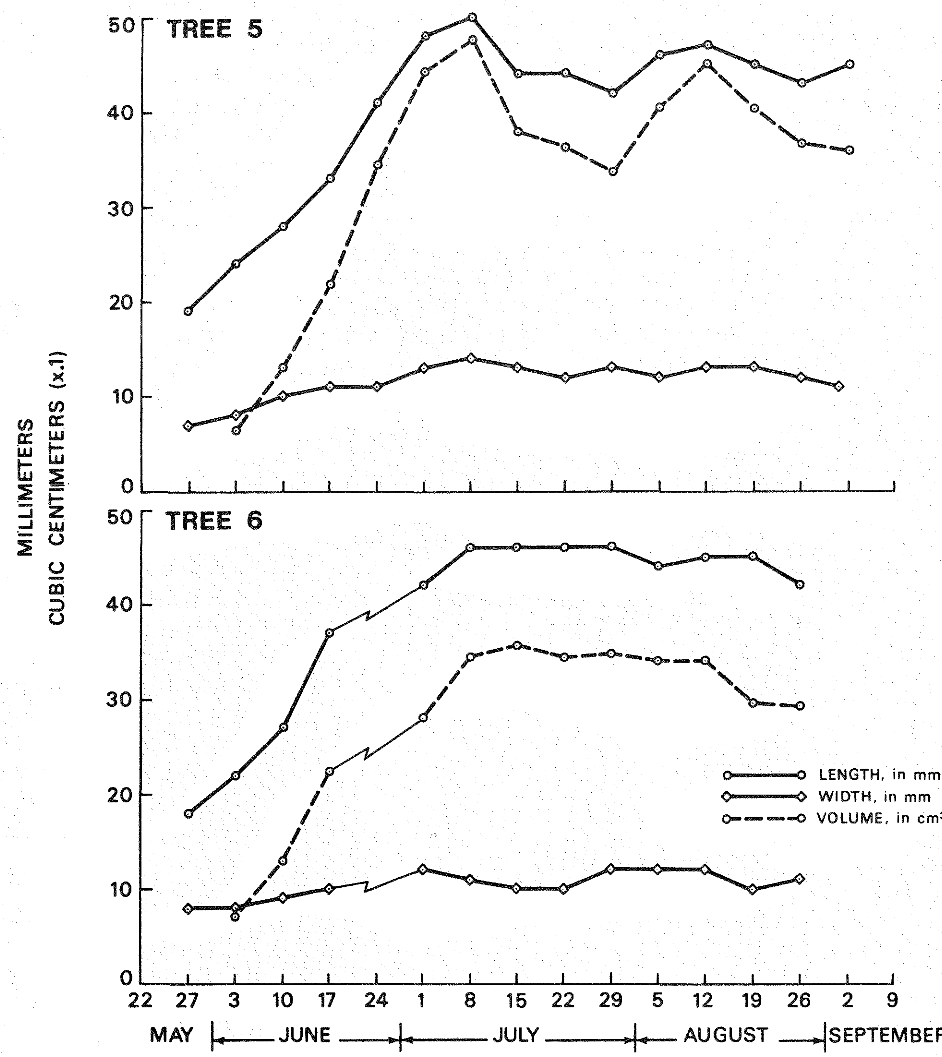


Figure 5.--Changes in volume, length, and width of white spruce cones during the 1970 growing season in Alaska.

Kenai Peninsula (stand 28), where Lutz spruce (*Picea* X*lutzii* Little), the natural hybrid between white and Sitka spruce *Picea sitchensis* (Bong.) Carr.), occurs. The smallest cones were found in both low elevation (stand 18, Fort Yukon) and high elevation (stand 29, Fielding Lake) stands.

The same pattern of variation may not exist from year to year. For example, figure 6 shows differences in the length of 1970 cones and those produced before 1970 for the 12-mile Summit stand (stand 17). The differences shown here may be extreme; examples of this magnitude, however, were observed in other stands.

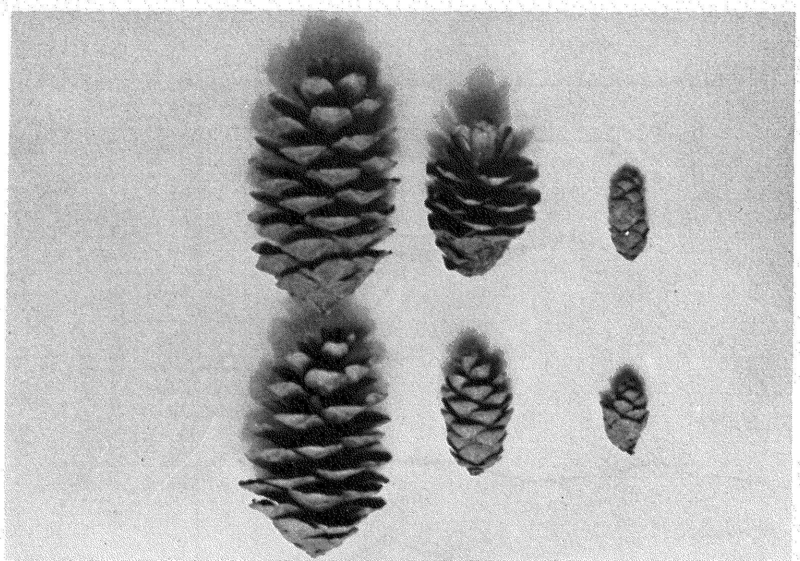


Figure 6.--Annual variation in size of cones from one tree. The two large cones on the left were formed before 1970, and the four smaller cones were produced in 1970 (collected in stand 17, 12-mile Summit).

The effect of environmental factors on cone elongation is probably similar to the effect on white spruce vegetative shoot elongation (determinate growth). One factor generally not considered in more southern coniferous forests which must be considered in these northern forests is that the cones of higher elevation stands in this study may have had their growth limited by the length of the growing season as well as by factors prevailing during the period when cones are actually expanding. As mentioned earlier, cone development in higher elevation stands (above 600 m) was at least 3 to 5 weeks behind that at 125 to 155 m.

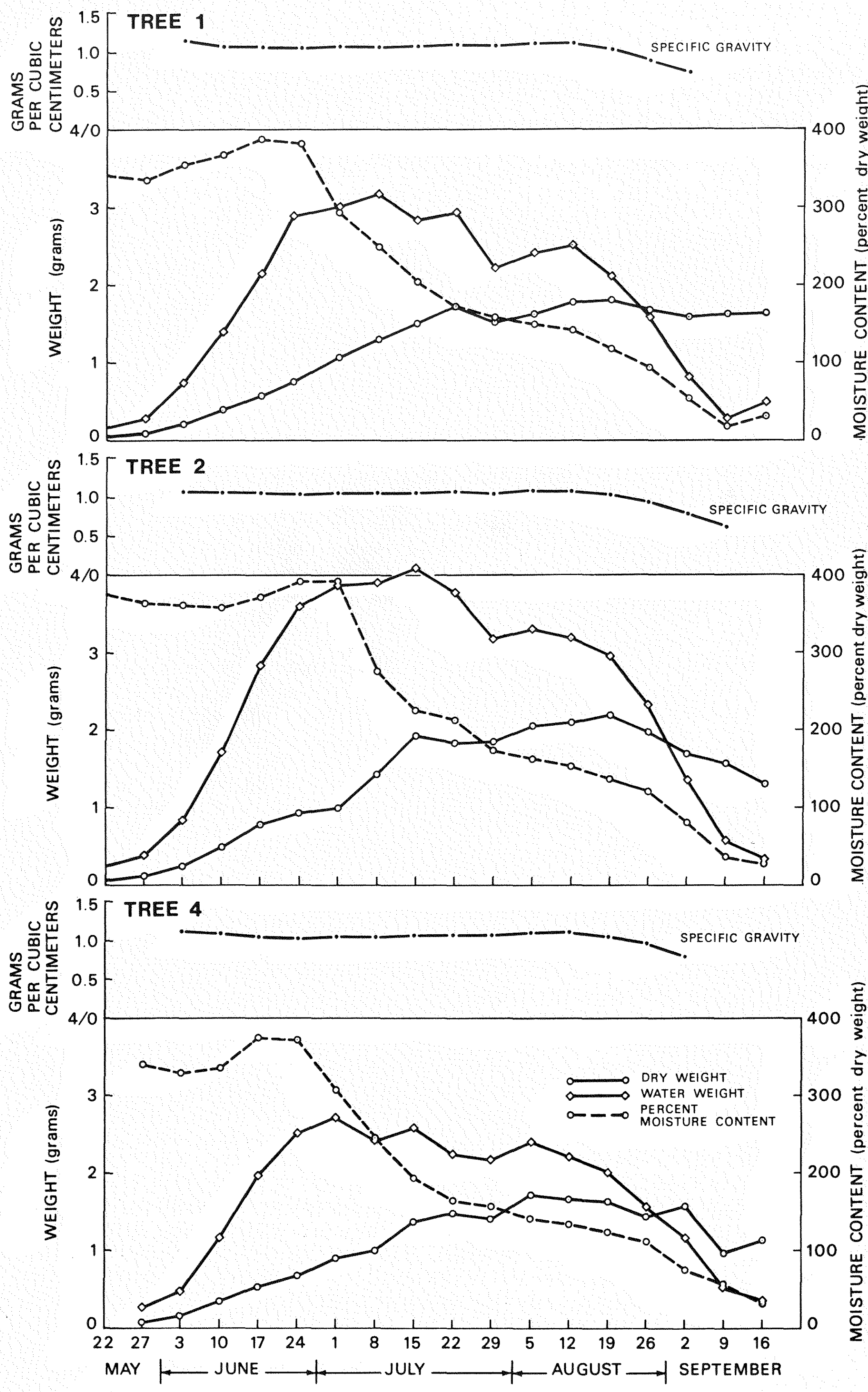
Seasonal patterns of changes in dry weight differed from those for water weight and percent moisture content. Dry weight increased gradually through late July or early August and then appeared to decrease during the several weeks prior to seed dispersal. Cone water content increased rapidly through early July, a pattern similar to that of changes observed in physical dimensions. After early July, water weight decreased until seed dispersal began; at this time water weight was similar to that of the young cones in late May (fig. 7).

Cone moisture content (percent of dry weight) was highest during June; it ranged from 300 to 400 percent. Clausen and Kozlowski (1965) reported a maximum moisture content of about 400 percent in late May and early June for white spruce in north-central Wisconsin. Beginning in early July, percent moisture content decreased. This decline was relatively rapid through mid-July. From mid-July to mid-August, moisture content decreased more slowly; rate of decrease accelerated from mid-August to seed fall. On September 2, shortly after seed dispersal began, percent moisture varied from 25 to 80 percent (fig. 7).

Changes in percent moisture content (dry weight basis) were not always associated with changes in cone water content (in grams). This was particularly noticeable during late June and early July, when percent moisture content began to decrease rapidly; at this time the cone water content was either increasing or relatively stable. Decrease in percent moisture at this time was associated with increasing dry weight of cones. This has been observed by Clausen and Kozlowski (1965) for white spruce, black spruce, larch (*Larix laricina* (Du Roi) K. Koch) and eastern hemlock (*Tsuga canadensis* (L.) Carr.). Changes in percent moisture were more closely associated with decreasing water weight after mid-August (fig. 7).

The relationship between cone development and seed development is the most important consideration from a practical standpoint. Three stages of seed development, are prefertilization, embryo enlargement, and the period between attainment of maximum embryo size and seed dispersal. Based on work by Rauter and Farrar (1969) indicating that fertilization in white spruce occurs about 3 weeks after pollination and on work by Fechner (1974) who reported that fertilization in blue spruce occurred 1 week after cones became pendent, we think the prefertilization period ended between June 17 and 24. Cones on trees in stand 1, T-field, become pendent about June 17. Embryo growth was completed by August 5 (Zasada 1973); seed dispersal began between September 2 and 10. When we compare these dates with the dates in figures 5 and 7 we see that, with the exception of cone dry weight, 90 percent or more of the cone growth occurred during or shortly after the prefertilization stage. There is little direct correlation between the attainment of seed maturity and changes in cone physical dimensions. The relationships which do occur appear to be between the attainment of critical levels of specific gravity and moisture content and seed maturation.

Crossley (1953) concluded that the most reliable indices of seed maturity in white spruce were cone firmness, seed coat color, and seed brittleness. Cone firmness was defined by Crossley as any degree of flexibility when the cone is squeezed between the thumb and finger. This criterion was met by the August 12 samples taken for this study. Changes


TREE 1
TREE 2
TREE 4
SPECIFIC GRAVITY
GRAMS PER CUBIC CENTIMETERS
WEIGHT (grams)
MOISTURE CONTENT (percent dry weight)
DRY WEIGHT
WATER WEIGHT
PERCENT MOISTURE CONTENT
1.5
1.0
0.5
4/0
3
2
1
0
400
300
200
100
22 27 3 10 17 24 1 8 15 22 29 5 12 19 26 2 9 16
MAY
JUNE
JULY
AUGUST
SEPTEMBER

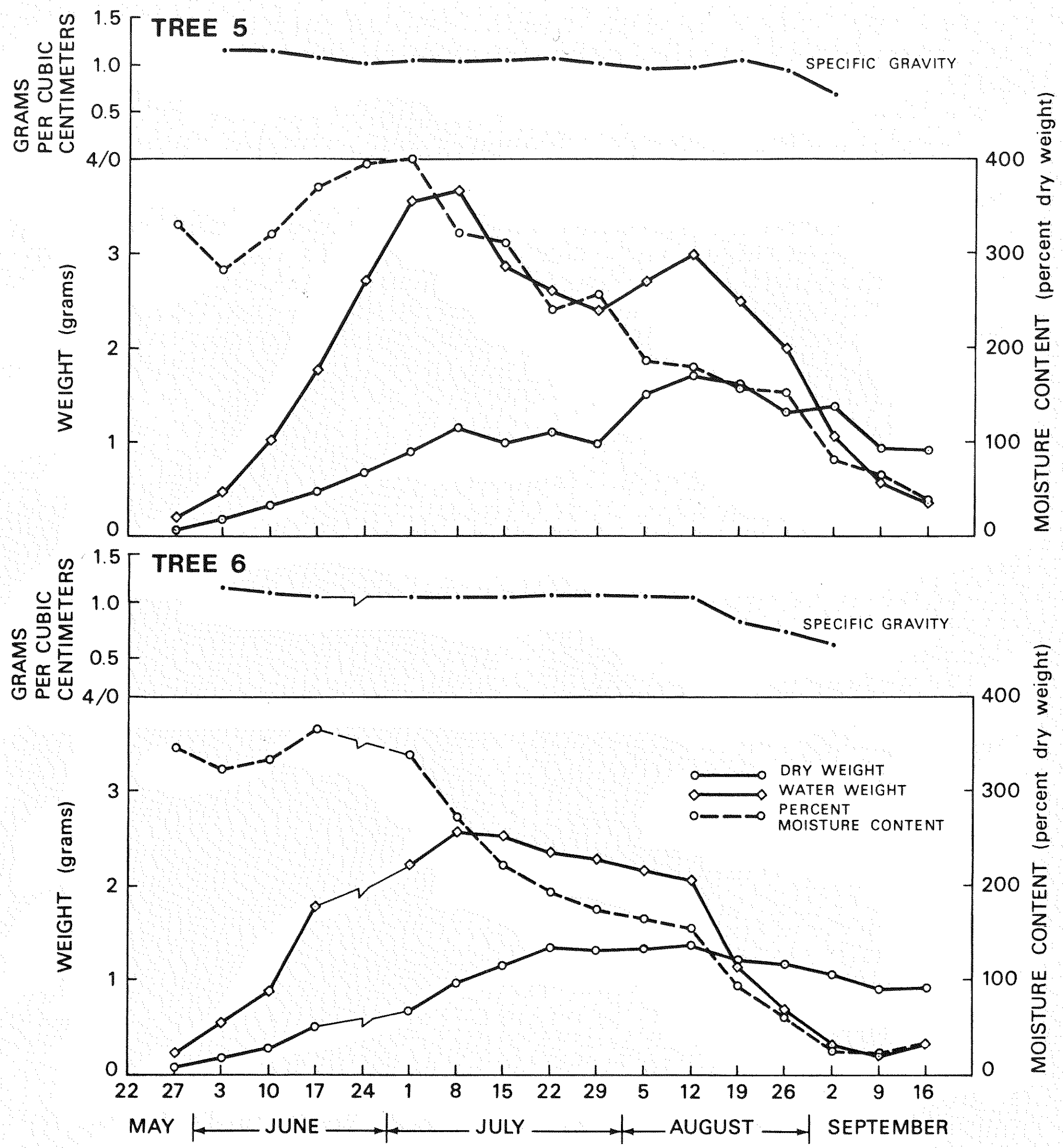


Figure 7.--Changes in dry weight, water weight, percent moisture content (dry weight basis), and specific gravity of white spruce cones from various trees during the 1970 growing season.

in seed coat color to dark brown or black and seed brittleness (seeds snap in two when cut with a sharp blade on firm surface), as defined by Crossley, also occurred on August 12.

In addition to normal cones, three abnormal cone types were observed. The most common was the bisexual cone. Cones with the female portion located at the apex were most common; only one out of many hundreds of these cones had the male portion at the apex. This abnormality was observed to a minor extent in many trees and was abundant in tree 5 in stand 1, T-field. Proliferated and forked cones were less common abnormalities (fig. 8). These cone types were reported in other North American conifers (Bingham et al. 1969, Edwards 1971).

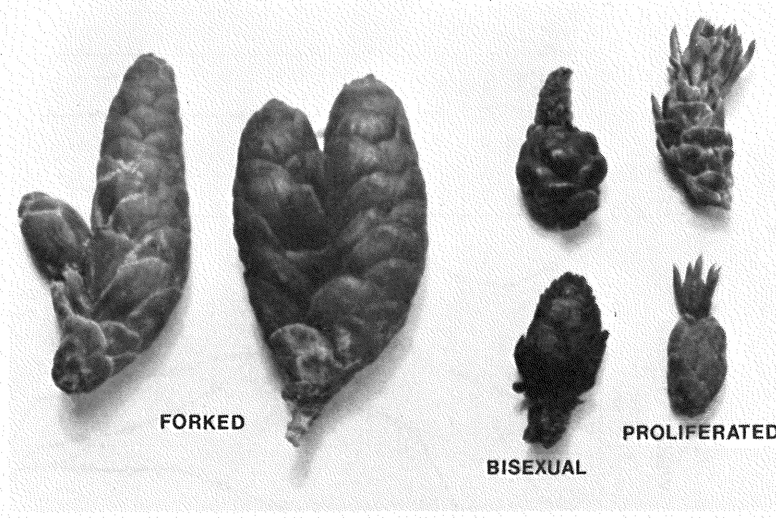


Figure 8.--Abnormal cones produced by white spruce in 1970 in Alaska.

Changes in color are an interesting aspect of white spruce cone development. White spruce cones may be green, pink, red, or a combination of these colors. The colors are most distinctive shortly after bud break. Cones enclosed in kraft bags to prevent pollination on a "red-coned" tree remained green. About 1 week after removal of the bag, the cones became the color of the rest of the cones on the tree, indicating a light-sensitive reaction. Teich (1970) suggested that color of female flowers in white spruce is controlled by a single gene.

The effects of insects on development were not assessed. Werner (1964) reported on white spruce cone and seed insects in Alaska.

Inland spruce cone rust (*Chrysomyxa pirolata*) was commonly observed in cones collected throughout the State in 1970. Areas from which rust could be identified are shown in figure 1. Nelson and Krebill (1970) reported that this

disease interferes with seed dispersal and lowers the viability of the seed. Ziller (1974) provides specific details concerning this disease.

SEED MATURITY

Seed maturation in arctic and subarctic forests of northern Europe and Russia is known to be limited by adverse weather conditions during the growing season (Gustafsson and Simak 1958, Norin 1958, Andersson 1965). No detailed studies on this subject have been reported in North America. This study was not designed to test this hypothesis for white spruce, but observations indicated that seed did not mature at certain locations in 1970.

Two general types of immaturity can be recognized. The most obvious immaturity occurs when female gametophyte and embryo are not fully developed at the macroscopic level; the female gametophytic tissue does not completely fill the seed or the embryo does not fill the embryo cavity or is otherwise deficient (for example, poorly developed cotyledons). The second general type of immaturity is biochemical; the development of the female gametophyte and embryo appears normal but the biochemical composition is not complete. In the observations described in the following discussion, only the first type of immaturity is quantified.

Methods

Seed ripening.--Cones collected in conjunction with those used for developmental observations were stored in sealed paper bags at room temperature (20°-22°C). Seeds were extracted and germination tests conducted in early September. Tests were conducted on stratified and unstratified seeds at 25°C with an 18-hour photoperiod for 30 days at a light intensity of 500 foot-candles. The tests were conducted on perlite in plastic boxes. Germination counts were made at 3- to 5-day intervals. A seed was considered germinated when the radicle had penetrated the perlite and the seed coat was raised off the seed bed. Seedlings were allowed to develop for the entire period of the test. After the tests were terminated, the ungerminated seeds were cut open to determine the percentage of filled seed.

Seed quality.--The white spruce stands from which seed was collected can best be described as mature stands which appeared to be representative of this forest type for a given area. No detailed stand descriptions were made. Cones were collected from at least four dominant trees in each of 29 stands (fig. 1). To obtain samples, trees were climbed or branch samples shot from the crowns. At least 20 cones from each tree were measured to the nearest millimeter. Prior to final drying and seed extraction, cones were stored

outside and protected from rain, a practice shown to improve germination of seed from immature cones (Zasada 1973). All collections were made within 2 weeks of seed dispersal at Fairbanks.

Final drying was at 20°-25°C for 2 weeks. Seeds were stored in sealed polyethylene bags at 1°-3°C for 1 year prior to germination testing. Seed weights were taken at the time of testing. Germination tests were conducted on four 100-seed replications from each seed lot for each of four trees for 30 days. At the end of the test period seeds were classified as follows:

1. Germinant with normal radicle and hypocotyl development, seed coat lifted off substrate. The majority of these had fully expanded cotyledons.

2. Germinant with radicle development but seed coat not lifted from substrate. Radicle was one to four times seed length.

3. Seed coat split and radicle less than length of seed.

4. Filled, inactive seed. These seeds had endosperm and embryo which appeared normal in cross-sectional view.

5. Filled but seed contents not normally developed. In many cases the endosperm and embryo had a mushy consistency.

6. Empty seeds.

Results and Discussion

Seed maturity in stand 1, (T-field), as indicated by changes in real germination of air-dried seeds collected at weekly intervals, increased from July 8 until early August (table 3). The attainment of relatively constant and high levels of germination preceded large decreases in cone water weight and specific gravity by 1 week or more.

The effect of stratification on germination of seeds at different stages of maturity can be summarized as follows. In 42 percent of the tests conducted before August 5, stratification increased germination. In the remaining cases, 50 percent (29 percent of total) showed decreases in germination due to stratification and the others were not affected. On August 5 and 12 germination of seed from these trees was significantly increased by stratification in only one case. In the August 19 and 26 and September 2 collections, differences between stratified and unstratified seed were from 1 to 7 percent (table 3).

Major changes occurred in endosperm and embryo appearance between early July and early August. After August 5, there appeared to be little change at the x-radiograph level of

resolution (fig. 9). A quantitative assessment of embryo growth (that is, elongation of embryo) indicated that enlargement ceased by August 5 (Zasada 1973). Rauter and Farrar (1969) reported that once the embryo ceased growth there were no further changes in anatomical structure.

Table 3--*Germination of stratified and unstratified white spruce seeds collected at weekly intervals in 1970*

Collection date and treatment	Tree 2	Tree 4	Tree 5	Tree 6
	Percent			
July 8:				
Stratified	0	0	0	6.6
Unstratified	0	0	0	14.6
July 15:				
Stratified	29.7	29.7	0	4.8
Unstratified	16.0	0	8.0	5.7
July 22:				
Stratified	44.8	54.0	18.2	60.6
Unstratified	23.0	34.3	47.5	35.9
July 29:				
Stratified	87.8	47.0	73.8	41.3
Unstratified	76.7	70.9	63.1	45.1
August 5:				
Stratified	94.4	83.3	86.9	70.5
Unstratified	93.4	86.4	88.9	89.7
August 12:				
Stratified	96.1	93.0	91.1	87.6
Unstratified	82.2	93.3	97.3	90.6
August 19:				
Stratified	98.5	94.6	94.7	89.7
Unstratified	91.6	91.2	90.8	90.6
August 26:				
Stratified	96.5	95.7	92.0	80.2
Unstratified	97.0	92.4	95.8	85.7
September 2:				
Stratified	95.2	91.3	90.7	--
Unstratified	97.6	90.9	96.3	--

Changes at the microscopic and biochemical levels were not examined; the results of a separate study (Zasada 1973), however, indicated significant changes. In this study, real germination of seeds dried at 40°C for 2 weeks was less than that of air-dried seeds until September 2 (seed fall began less than 1 week later). Although the stress created by the 40°C treatment was relatively severe, the results did show that the closer the collection date was to seed fall the better the seed could withstand the stress.

Phenological observations in the Alaska Range transect, germination testing, seed dissection, and x-radiography

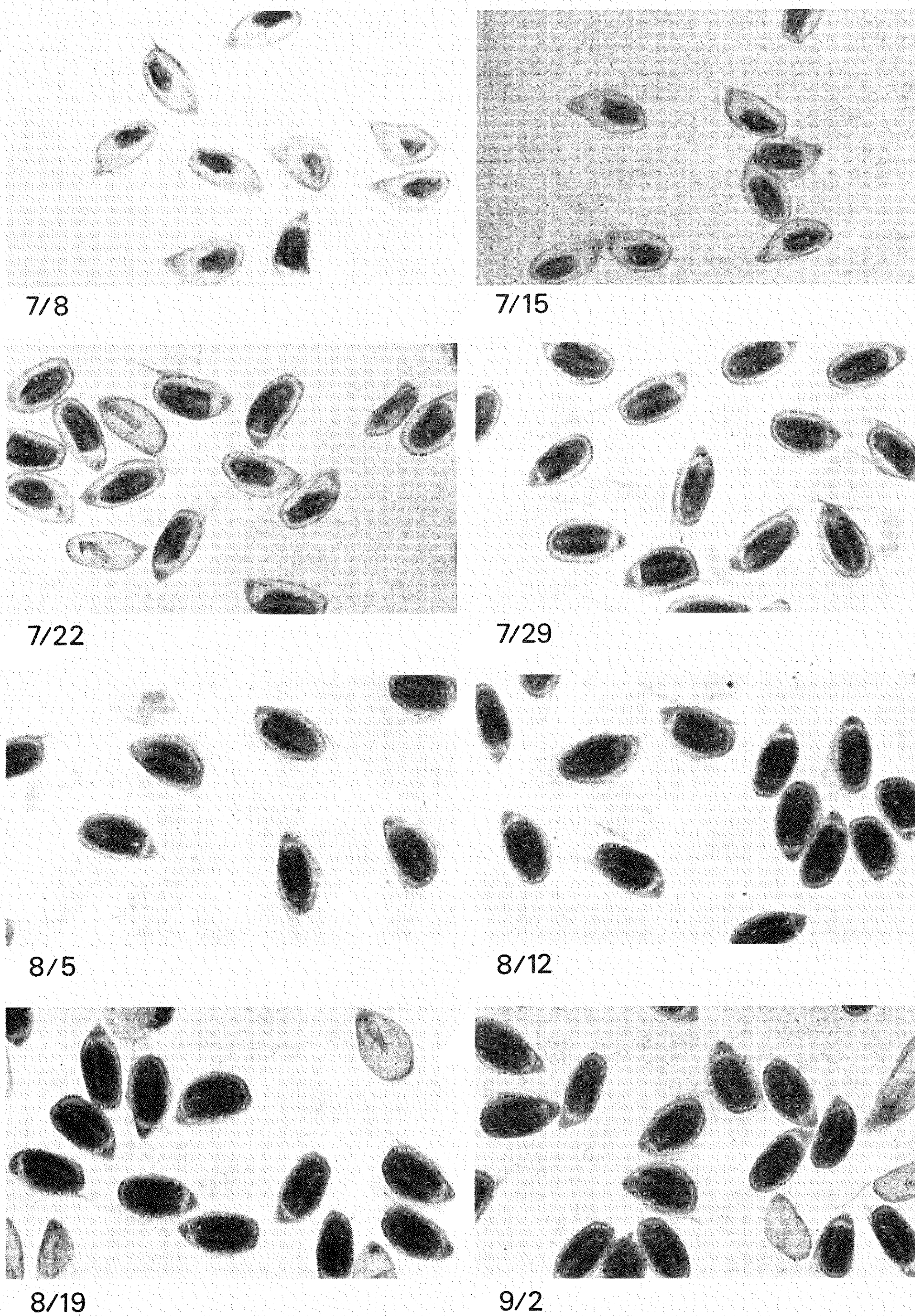


Figure 9.--Endosperm condition, as indicated by x-radiography, in air-dried seeds of white spruce collected at weekly intervals. Radiograph for August 26 is not included as development was same as September 2.

provided further information on seed maturity. Phenological observations indicated that flowering was delayed by as much as 5 weeks at higher elevations. Although this much delay is observed in other mountainous regions, it becomes particularly critical in interior Alaska where growing seasons are normally 90 to 100 days or less. Stands in which phenology was most delayed did not produce mature seed.

The germination and cutting tests indicated a wide range of variation in germinability and seed quality within and between stands (tables 4 and 5). The highest germination (80 percent or higher) occurred in three stands--stand 1 (T-field), stand 4 (Bonanza Creek-2), and stand 5 (Thinning Area)--in the Fairbanks area and in one--stand 15 (Yukon River-1)--on the Yukon River east of Fairbanks. Use of germinability as an indication of seed quality was complicated by the occurrence, in the majority of seed lots, of large numbers of seed which either had split seed coats or were filled but showed no sign of activity.

Although stratification is not recommended for testing white spruce seed (International Seed Testing Association 1966), Wang (1974) has reported that dormancy in white spruce seed may vary with seed source and that prechilling from 21 to 28 days resulted in maximum laboratory germination and superior nursery germination and seedling survival. In tests of five seed lots conducted in 1974, stratification produced a threefold increase in germination in the lots from the Black Rapids (stand 9) and Delta Junction (stand 7) stands but had no measurable effect on the lots from Bonanza Creek-3 (stand 6) and Chena River (stand 3) (table 6). In addition, stratification improved germination in some of the immature seed collected in stand 1 (T-field) (table 3).

Because of the results of the stratification tests and because the endosperm and embryos of imbibed seeds (30 days at germination temperature) were usually adequate to be classified as filled seed, 100 or more filled unimbibed seeds from 18 of the 29 seed lots were dissected. Embryos and endosperm were classified according to criteria of Simak (1957). Of the 17 lots examined, 6 contained a large percentage of seeds with immature embryos and/or poorly developed endosperm (table 5). The embryos which filled the embryo cavities in these six collections (class IV) had poorly developed cotyledons. Of these stands, four were located at 615 m or higher in the Alaska Range, one at 770 m in the White Mountains, and two north of the Arctic Circle. Lower elevation stands with real germination of less than 40 percent had seed with fully developed embryos and endosperms (tables 4 and 5). These data, plus data on the effect of stratification, indicated that biochemical immaturity may occur in some seed lots. From these findings, we recommend that, until the white spruce dormancy pattern is understood in more detail, all lots of white spruce seed from Alaska should be subjected to stratified and unstratified germination tests prior to sowing.

Table 4--*Germination of Alaskan white spruce seed from 1970 seed crop*[1/]

Stand number	Area	Germination	Radicle 4 times seed length	Split seed	Filled, inactive seed	Empty seed[4/]
				Percent		
1	T-field	85.0 ± 2.8[3/]	5.4 ± 4.0	8.4 ± 2.8	1.2 ± 1.2	7.5 ± 4.9
2	Bonanza Creek-1	67.9 ± 10.3	3.0 ± 2.1	16.7 ± 7.4	12.4 ± 13.6	7.2 ± 4.2
3	Chena River	61.7 ± 22.6	3.6 ± .8	27.0 ± 20.8	7.7 ± 4.2	9.0 ± 5.1
4	Bonanza Creek-2	85.0 ± 10.9	2.5 ± 2.4	5.8 ± 3.4	6.7 ± 6.8	2.0 ± 1.6
5	Thinning Area	81.4 ± 13.4	3.4 ± 1.9	11.8 ± 10.5	3.4 ± 2.0	12.5 ± 4.6
6	Bonanza Creek-3	64.8 ± 14.0	7.2 ± 2.4	15.9 ± 8.7	12.1 ± 7.8	14.5 ± 3.9
7	Delta Junction	33.7 ± 20.1	4.9 ± 1.9	42.5 ± 18.2	18.9 ± 17.4	11.2 ± 5.3
8	Gerstle River	67.6 ± 14.7	9.8 ± 2.5	19.5 ± 10.9	3.1 ± 2.4	2.0 ± 1.1
9	Black Rapids	24.4 ± 11.1	8.4 ± 2.2	40.3 ± 11.8	26.9 ± 14.6	13.0 ± 8.7
10	Klutina River-1	26.8 ± 7.7	6.5 ± 4.2	41.1 ± 22.3	25.6 ± 12.9	2.2 ± .6
11	Klutina River-2	12.4 ± 11.3	5.2 ± 2.0	44.2 ± 12.0	38.2 ± 15.2	14.2 ± 9.8
12	Tok	24.9 ± 18.5	6.3 ± 3.2	39.1 ± 8.8	29.7 ± 13.0	16.2 ± 10.3
13	40-mile	29.5 ± 16.8	3.5 ± 2.8	53.7 ± 20.3	13.3 ± 6.9	14.2 ± 4.9
14	Eagle	42.6 ± 3.8	5.7 ± 2.6	26.0 ± 16.0	25.7 ± 20.9	2.8 ± 1.6
15	Yukon River-1	84.3 ± 15.5	3.0 ± 1.5	11.4 ± 15.4	1.3 ± 1.3	1.2 ± 1.0
16	Yukon River-2	68.0 ± 8.8	4.1 ± 2.7	19.5 ± 8.9	8.4 ± 8.3	6.0 ± 2.4
17	12-mile Summit	0	2.2 ± 4.6	62.4 ± 25.7	35.4 ± 21.7	15.0 ± 6.6
18	Fort Yukon	39.3 ± 6.8	5.8 ± 2.0	40.1 ± 7.7	14.8 ± 4.2	6.7 ± 1.3
19	Wiseman	30.6 ± 16.5	6.2 ± 4.2	52.9 ± 19.0	10.3 ± 5.2	26.8 ± 15.8
20	Kobuk	35.5 ± 21.0	7.3 ± 5.1	45.8 ± 11.3	11.4 ± 13.5	9.8 ± 3.2
21	Kiana	37.0 ± 16.0	5.2 ± 3.2	38.6 ± 20.8	19.2 ± 7.8	23.8 ± 6.0
22	Nulato	53.0 ± 22.0	3.3 ± 1.0	24.0 ± 19.9	19.7 ± 26.0	14.8 ± 6.0
23	Ruby	63.1 ± 17.6	6.4 ± 3.9	15.8 ± 9.6	14.7 ± 12.7	24.0 ± 16.8
24	Tanana	70.6 ± 17.2	2.2 ± 1.4	20.9 ± 11.4	6.3 ± 9.4	5.5 ± 1.2
25	Kantishna	4.5 ± 2.5	3.3 ± 3.3	72.2 ± 8.7	20.0 ± 9.1	23.8 ± 5.1
26	Deneki Lakes	0	2.9 ± 5.0	56.9 ± 35.9	40.2 ± 31.3	9.2 ± 4.8
27	Anchorage	54.3 ± 29.3	4.1 ± 1.4	25.4 ± 25.1	16.2 ± 26.8	25.0 ± 7.3
28	Kenai	14.9 ± 13.5	8.6 ± 1.6	42.0 ± 27.4	34.5 ± 36.2	40.2 ± 9.8
29	Fielding Lake[2/]	--	--	--	--	--

[1/] First 4 data columns are based on filled seed fraction only. The empty seed column gives the average number of empty seeds per 100-seed replication.

[2/] Fielding Lake seed not germinated. No observed seed contained embryos.

[3/] Standard deviation.

[4/] Includes empty seeds and those with poorly developed endosperm and embryo. The latter seeds often had a "mushy" consistency.

Table 5--*Embryo and endosperm condition as determined by dissection of seed*

(Percent of seeds)

Stand area	Embryo[1]				Endosperm[2]	
	I	II	III	IV	A	B
Bonanza Creek-1	0	0	0	100.0	100.0	0
Bonanza Creek-2	0	0	0	100.0	100.0	0
Bonanza Creek-3	0	0	0	100.0	100.0	0
Delta Junction	0	0	0	100.0	100.0	0
Gerstle River	0	0	0	100.0	100.0	0
Black Rapids	27.3	22.7	19.3	30.7	76.9	23.1
Tok	3.4	17.5	25.8	53.3	85.0	15.0
Eagle	3.1	0	0	96.9	95.9	4.1
Yukon River-1	0	0	0	100.0	100.0	0
Yukon River-2	0	0	0	100.0	100.0	0
12-mile Summit	75.0	25.0	0	0	0	100.0
Fort Yukon	0	0	0	100.0	100.0	0
Wiseman	12.5	5.7	20.4	61.4	90.9	0
Kobuk	0	0	0	100.0	100.0	0
Kiana	31.7	6.6	3.3	58.9	57.5	42.5
Deneki Lakes	64.2	35.8	0	0	29.3	70.7
Anchorage	2.5	0	5.0	92.5	98.8	1.2
Fielding Lake	100.0	0	0	0	0	100.0

1/ Embryo class: I = Endosperm but no embryo; II = endosperm and one or several embryos, none of which is longer than half of the embryo cavity; III = endosperm and one or more embryos, the longest of which measures between half and three quarters of the embryo cavity; IV = endosperm with one fully developed embryo, completely or almost completely occupying the embryo cavity.

2/ Endosperm class: A = The endosperm almost fills the seed coat to capacity. B = The endosperm does not fill the seed coat and is often shrunken or otherwise deformed.

Table 6--*Effect of stratification on real germination of Alaskan spruce seed*

Stand area	Stratified seed	Unstratified seed
	Percent real germination	
Chena River	97	93
Bonanza Creek-3	74	72
Delta Junction	95	31
Gerstle River	94	82
Black Rapids	68	22

Seed weight for the sources from which data were available ranged from 0.11 to 0.25 gram per 100 seeds (table 7). This range of seed weight falls within the ranges reported for white spruce by Hellum (1969) (0.13 to 0.32 gram per 100 seeds) and Safford (1974) (0.11 to 0.34 gram per 100 seeds). A comparison of average weights, however, indicates that average weight of Alaska seed (0.16 gram per 100 seeds) is less than that reported by Hellum (1969) (0.23 gram per 100 seeds) and Safford (1974) (0.20 gram per 100 seeds). It must be stressed that the seed lots in this study and those of Hellum (1969) and Safford (1974) may not be strictly comparable because of differences in such variables as percent filled seed and moisture content. Norin (1958) regarded low seed weights (0.12 to 0.26 gram per 100 seeds) for *Picea obovata* at similar latitudes in Russia as an indication of immaturity.

The correlation between seed quality as measured by real germination and seed weight for these data is poor. For example, stands Yukon River-1 (stand 15), Bonanza Creek-2 (stand 4), and T-field (stand 1), with the highest real germination, differed markedly in seed weight (0.1140, 0.1149, and 0.2302 gram per 100 seeds). Similarly, elevation and seed weight did not appear to be correlated.

These observations show that some stands in Alaska do not produce seed with mature embryos every year. Since these observations in 1970, we have observed seed immaturity in some of the same stands. On the other hand, seeds with immature embryos have not been observed in the Tanana Valley spruce stands during an 8-year period.

Table 7--*Seed weight*[1] *for Alaskan white spruce seed collected in 1970*

Stand area	Seed weight per 100 seeds and standard error	N[2]
	------ Grams ------	
T-field	0.1149 ± 0.0001	2
Bonanza Creek-1	.2174 ± .0221	2
Chena River	.1145 ± .0001	2
Bonanza Creek-2	.2302 ± .0343	4
Thinning area	.1860 ± .0240	1
Delta Junction	.2290 ± .0766	2
Gerstle River	.2052 ± .0116	4
Black Rapids	.1138 ± .0006	2
Klutina River-1	.1138 ± .0001	2
Tok	.1648 ± .0101	2
40-mile	.1141 ± .0002	1
Eagle	.1149 ± .0002	3
Yukon River-1	.1140 ± .0002	4
Yukon River-2	.1147 ± .0002	3
12-mile Summit	.1223 ± .0023	1
Fort Yukon	.2040 ± .0088	1
Wiseman	.1139 ± .0001	1
Kobuk	.1143 ± .0001	1
Nulato	.2489 ± .0477	2
Ruby	.2368 ± .0094	1
Tanana	.2411 ± .0414	2
Deneki Lakes	.1138 ± .0001	2

[1] Only seed lots with less than 5 percent empty seed were used.

[2] N indicates the number of trees from which seed could be used for weight determination.

CONE PRODUCTION AND SEED DISPERSAL

Cone Production

Counting of cones is easiest and counts are most accurate in July after cones have attained maximum size and well before squirrels begin to harvest them. Because environmental conditions (for example, frost) can reduce cone numbers, the cones observed in July may not be an adequate estimate of the number of cones at bud break. For insight into the problem of cone mortality, the following observations were made:

For an estimate of cone losses, 100 cones were tagged about June 1 on each of six trees. These cones were examined periodically and recounted in August. The death of a single

cone on each of two of these trees before June 1 was the only reduction in cone number that occurred. Although Zasada (1971) observed significant cone losses caused by subfreezing temperatures in 1970, a frost which occurred in stands 1 (T-field) and 3 (Chena River) did not result in observable damage. Temperatures at this time (June 9) dropped to -2°C for 4 to 6 hours. These subfreezing temperatures occurred at a time when the cones were relatively resistant to mild freezing (Zasada 1971).

A further test was conducted to determine if absence of pollination resulted in cone mortality, as Sarvas (1957) reported for Scotch pine (*Pinus sylvestris* L.). Two branches from three of the trees observed for cone survival were enclosed in a pollination bag before pollen dispersal began. Fifty cones on each tree were treated in this manner. After these cones were no longer receptive, the bags were removed; in August the cones were collected and counted and seeds examined. None of the cones had died. X-ray analysis revealed no filled seeds in unpollinated cones (fig. 10). The cones from the unpollinated branches were much smaller than those exposed to open pollination, but no other morphological differences were observed.

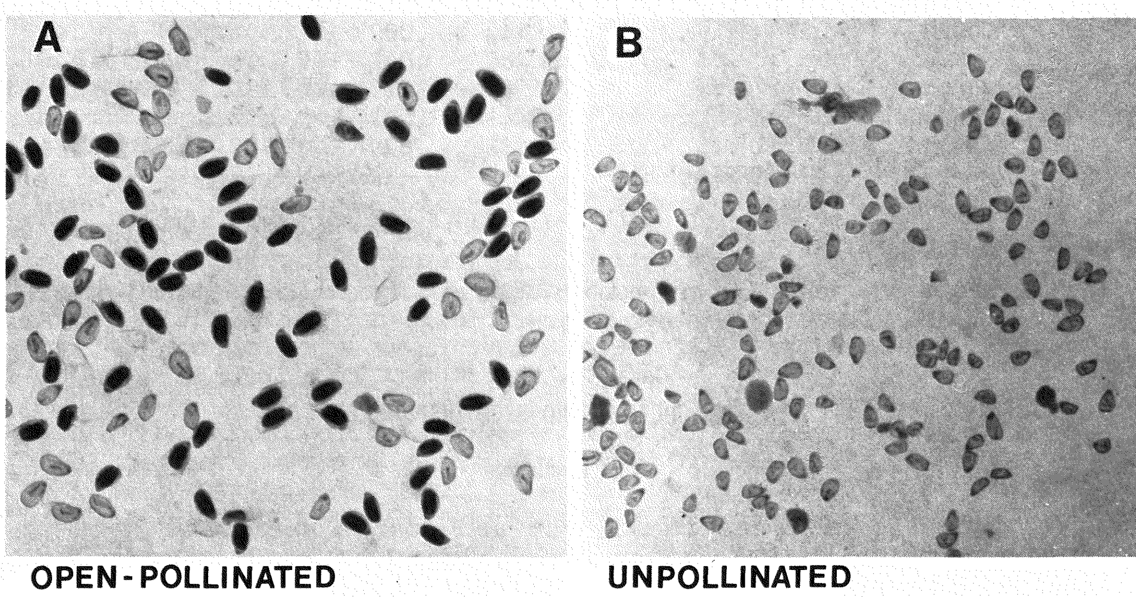


Figure 10.--Seed produced by (A) open-pollinated and (B) unpollinated white spruce cones.

In summary, although a mild frost occurred in some stands about 2 weeks after pollination, there was no evidence of frost damage to the cone crops in any stand in which cones were counted. No cone mortality was observed on six sample trees, and nonpollination did not result in cone mortality. Thus, at least for 1970, the number of cones on the trees at the time of the cone counts was a good estimate of the number of cones at the time of bud break.

In each stand where seed traps were located (table 1), 15 or 16 trees were selected and partial cone counts were made. The counts were made from one point with a variable power (15X to 60X) spotting telescope. Thus, the total cone crop is not represented, only the number of cones visible from one side of the tree. The number of cones counted can be considered only an approximation of the actual number because of the difficulty of seeing all cones. The accuracy of the approximation decreases as the number of cones produced increases. Problems associated with accuracy of cone counts are discussed by Machaniček (1973).

These counts indicated that no tree in any stand (except stand 16) had fewer than 100 cones and that most trees had 300-500 or more cones. In stands 2, 3, 4, 6, and 15 (Bonanza Creek-1, Chena River, Bonanza Creek-2, Bonanza Creek-3, and Yukon River-1), some trees had a minimum of 800-1,500 cones per tree (table 8).

Table 8--*Number of cones produced*[1/] *in mature white spruce stands in Alaska in 1970*

Tree number	Stand area							
	Bonanza Creek-1	Bonanza Creek-2	Bonanza Creek-3	Chena River	Klutina River-1	Klutina River-2	Yukon River-1	Yukon River-2
1	350	800	420	1,280	500	500	434	29
2	800	1,100	406	1,560	124	321	133	390
3	327	1,300	338	610	240	260	619	40
4	350	700	230	848	250	377	361	433
5	756	550	121	905	350	469	600	228
6	652	585	177	856	322	207	374	514
7	602	415	416	808	173	209	405	152
8	600	775	309	932	460	986	329	176
9	500	419	530	1,000	270	445	475	440
10	100	360	806	730	200	415	410	467
11	482	217	950	705	371	282	900	258
12	434	400	930	560	288	503	585	271
13	300	850	310	448	500	170	800	500
14	436	900	418	800	400	258	390	350
15	421	470	522	219	272	643	500	132
16	400	--	--	--	216	--	--	--

1/ Number of cones visible on one side of the tree.

All stands had some cones harvested by squirrels. In all but stand 3 (Chena River), however, the squirrels appeared to reduce the number of cones only slightly. In stand 3, cone counts made in early September showed that the crops of all but one-third of the trees had been reduced by 80 percent or more. Based on cone count data, this stand had at least as many cones originally as other stands. Stand 3, however, ranked last among undisturbed stands in the total amount of seed dispersed (table 9).

Table 9--*1970 seed fall in Alaskan white spruce stands*

Stand area	Number of seeds per square meter	Number of filled seeds per square meter	Filled seeds
			- - Percent - -
Bonanza Creek-1	1,003	609	60.7
Bonanza Creek-2	2,068	1,595	77.1
Bonanza Creek-3	1,038	615	59.2
Chena River	252	128	50.8
T-field	1,121	635	56.6
Thinning Area	950	431	45.4
Klutina River-1	2,076	1,100	53.0
Klutina River-2	415	157	37.8
Chena (cutover)	31	16	51.6
Clayton (cutover)	435	294	67.6

Seed Production and Dispersal

METHODS

For observation of seed fall, ten 0.5-square-meter, funnel-shaped seed traps were placed in each of 12 stands. Ten of these stands were undisturbed (table 1) and two were cutovers. Stands 15 and 16 (Yukon River 1 and 2) were flooded during spring breakup in 1971 and yielded no seed fall data. The sampling surface was located about 1.4 meters above the ground. In all stands the traps were serviced in July or August 1970. In stands 2 and 3 (Bonanza Creek-1 and Chena River), collections were made from the traps at 7- to 10-day intervals from August until January and at about monthly intervals thereafter. The last collection was in early August 1972. In the other stands, collections were made in early November 1970 and late July 1971. After collection, the seeds were separated from the litter and counted. Filled seed percentage was determined by a cutting test. Only seeds containing an embryo and more than three-fourths filled by the endosperm were classed as filled.

RESULTS AND DISCUSSION

Seed dispersal in the study trees in stand 1, T-field, had started by September 2, about 99 days after pollen dispersal (this assumes that pollination occurred on May 26). Cram and Worden (1957) reported 97-99 days and Crossley (1953) 108 days. Tree 6 was most advanced in this respect; all but a few cones were open and dispersing seed on September 2. Trees 2, 4, and 5 had not dispersed seed on September 2; by September 10, however, 50 percent or more of the cones on these trees were open and dispersing seed. Tree 1 was intermediate with a few cones open on September 2 and all cones dispersing seed by September 10.

The start of seed dispersal as measured by weekly collections from seed traps in stands 2 and 3 (Bonanza Creek-1 and Chena River) agreed with observations in stand 1 (T-field). The first significant quantity of seed was dispersed in stand 2 between September 3 and 10; in stand 3, between September 1 and 8.

The seasonal pattern of dispersal observed is similar to that reported for these same stands in 1968 (Zasada and Viereck 1970) (fig. 11, table 10). Although the majority of the seed was dispersed prior to January, there were still significant amounts of filled seed (7 and 15 percent) remaining in the cones. During a good seed year such as 1970, this quantity of seed could be adequate for seeding winter scarified seed beds. The seed dispersed from September 1971 through August 1972 is attributed to the 1970 crop because no cone production was observed in 1971.

Table 10--*Cumulative dispersal of the 1970 seed crop*

(In percent)

Stand, seed fall, and filled seed	1970					1971							From Sept. 1971 to Aug. 1972
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July-Aug.	
Stand 2:													
Total seed fall	0.5	51.5	68.1	86.8	87.2	88.4	89.5	91.7	94.5	97.3	97.9	98.0	100.0
Filled seed	0	57.8	73.3	91.2	92.6	93.3	94.1	95.4	96.7	98.4	98.6	98.7	100.0
Stand 3:													
Total seed fall	4.3	46.0	60.9	75.5	80.0	83.4	85.1	92.8	95.1	95.7	96.8	97.4	100.0
Filled seed	3.6	56.2	68.4	75.2	83.1	85.5	86.7	95.2	98.2	98.8	99.4	99.4	100.0

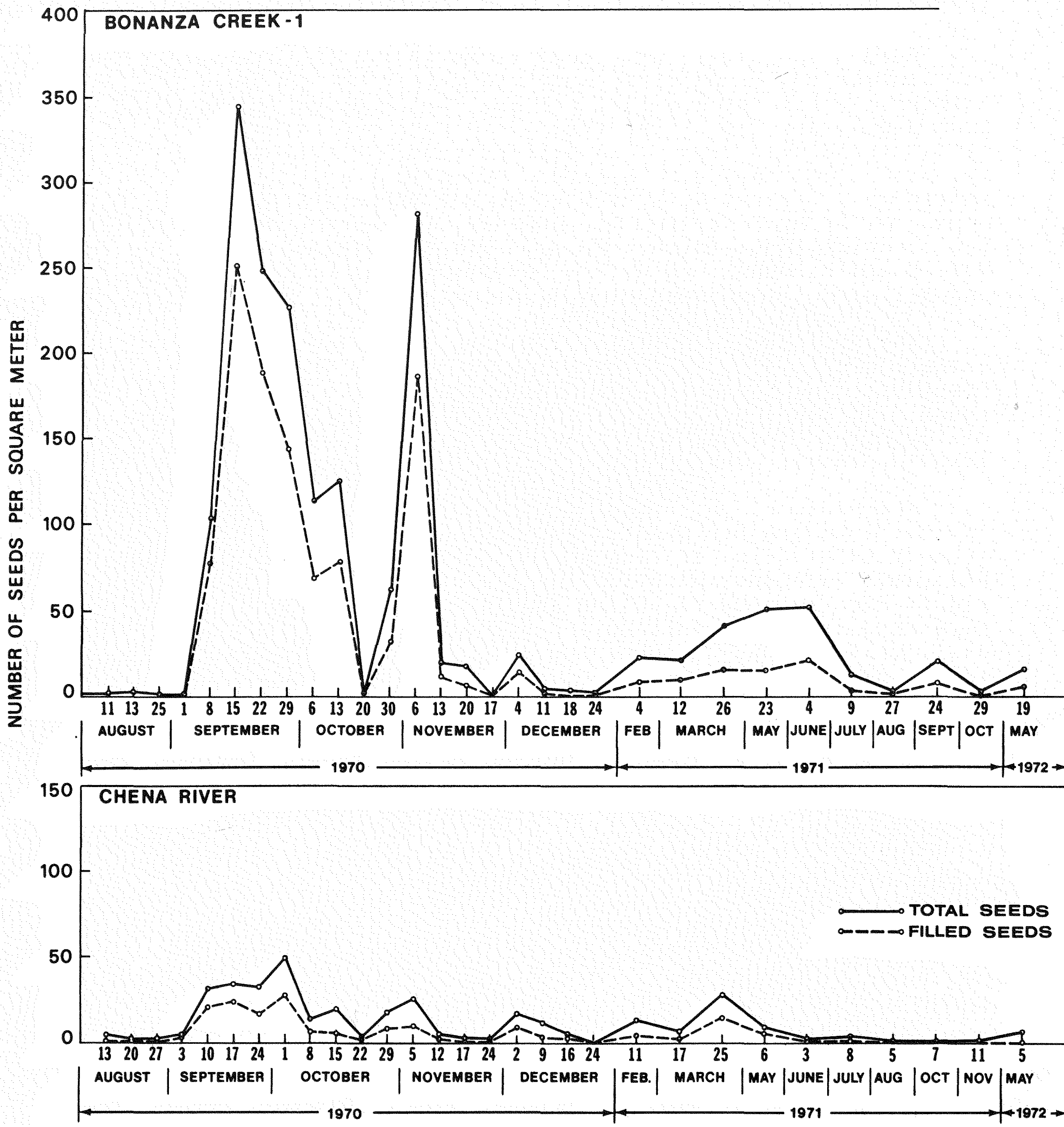


Figure 11.--Annual seed dispersal in two mature white spruce stands (stand 2, Bonanza Creek-1, and stand 3, Chena River).

Total seed fall in all undisturbed stands was greater than 250 seeds per square meter (1 million per acre). Greatest production was about 2,000 seeds per square meter (8 million per acre) in stands 4 (Bonanza Creek-2) and 10 (Klutina River-1). Stands 4 and 10 produced the greatest quantity of filled seed (table 9). In 1958, the last excellent seed year, the estimated production in stand 4 was approximately twice that in 1970 (Zasada and Viereck 1970). In two partially cut white spruce stands, seed fall estimates were 31 (total) and 16 filled seeds per square meter (128,000 and 66,000 per acre) and 435 and 294 seeds per square meter (1.8 million and 1.2 million per acre). The largest spruce seed crop reported in North America of 5,450 (total) and 3,030 filled seeds per square meter was for red spruce (*Picea rubens* Sarg.) in New Brunswick (Powell 1975).

Germination and Seedling Establishment

The final phase of the natural regeneration portion of forest management begins as soon as the seed lands on the seed bed. From this time until the seedling becomes established, a complex set of biological, physical, and chemical variables interact with the seed and the various stages of seedling development to determine the success or failure of regeneration. The observations made in this study were primarily concerned with the dynamics of the white spruce seedling population on a mineral soil seed bed over a 5-year period. The most detailed observations were made of germination and 1st-year survival and selected physical environmental variables. Similar observations were made for paper birch because this species is one of the major trees associated with white spruce in interior Alaska. A knowledge of the regeneration potential of birch is critical to a thorough understanding of white spruce management. The changes in other plant species associated with changes in the white spruce seedling population were also recorded.

Although white spruce has been used for firewood, house logs, mine timbers, and lumber in interior Alaska since the early 1900's, little thought was given to securing natural regeneration. To our knowledge our study was the first formal attempt to obtain natural regeneration of white spruce in Alaska; thus, one of the main objectives of this study was to provide a small-scale demonstration of the regeneration potential during an excellent seed year. A secondary objective was to test methods for assessing natural regeneration in a larger study which began in 1972.

METHODS

The area for the natural regeneration part of our study is an upland site in the Bonanza Creek Expérimental Forest located 15 km southwest of Fairbanks, Alaska, and 0.5 km from stand 4, Bonanza Creek-2. This area is a gently sloping

(approximately 10-percent slope) south-southwest-facing site, typical of upland white spruce sites in this area. The original stand contained 75-percent white spruce and 25-percent paper birch. The soil is a deep phase of the Fairbanks silt loam series and has developed in loess parent material.

In July 1970 a 0.59-hectare (77- by 77-m) area was cleared of all vegetation except for several dominant white spruce which were left as a seed source. Within this larger clearing, a 0.1-hectare (31- by 31-m) area was cleared of all organic matter. Five 0.5-square meter seed traps were used to estimate seed fall. These traps were emptied annually after snowmelt in late April or May and in August. Percent filled seed was estimated from cutting tests. Viability of filled seed in stand 4 (Bonanza Creek-2) was 85 percent (table 4). Figure 12 shows the general nature of the study area and the vegetation recovery at the end of the third growing season.

Figure 12.--General view of a portion of the forest opening in which seedling establishment was observed (A). Note vegetative recovery after 3 years (B). The funnel-shaped seed trap is an example of traps used in the seed fall observations in this area and in the 12 stands mentioned earlier.

Plots for observation of seed germination and seedling survival and general vegetative development were established on mineral soil shortly after site preparation. Spruce seedling plots were 60 cm in diameter (0.283 square meter) and birch plots were 20 cm (0.031 square meter); 20 plots were used for each species. The total number of seedlings on which the observations are based is shown in table 11.

Table 11--*Number of first growing season germinants and surviving seedlings produced during the 1st, 2d, 3d, and 5th growing seasons*

Germinants	1971				1972	1973	1974 and 1975
	May-June	July	August	Total			
White spruce:							
Total germinants	605	549	265	1,419	0	--	--
Survivors after 1 growing season	325	458	189	972	0	194	0
Paper birch:							
Total germinants	331	302	197	830	--	--	--
Survivors after 1 growing season	163	221	128	512	72	86	0

During the first growing season (1971), weekly observations were made from mid-May through September. New seedlings were marked with toothpicks. During 1972, observations were made in the early summer and fall; in 1973 and 1975 in the fall only. Changes in cover and frequency of vascular and nonvascular plants were observed in twelve 1 m^2 plots in August of 1971, 1972, 1973, and 1975. Seedling growth observations consisted of weekly excavations of seedlings during 1971. The seedlings which were excavated represented the most well-developed seedlings within the study area. Development was assessed on the basis of aboveground growth.

Soil temperatures were monitored in the area during the first growing season using Tempils[1/] and thermistors. Rainfall data were obtained from a weather station located in a similar opening about 1 km from the study area (Barney and

[1/] The use of trade, firm, or corporation names is for the convenience of the reader and does not constitute an official endorsement by the U.S. Department of Agriculture.

Berglund 1973). Weekly soil moisture determinations were made gravimetrically at 0- to 2-, 3- to 5-, and 6- to 8-cm depths; moisture measurements were replicated four times. The soil sampler used was 4 cm in diameter. Soil moisture content was converted from a weight basis to a volume basis.

RESULTS AND DISCUSSION

Germination

Germination of white spruce and paper birch seed began between May 21 and May 28, 1971; the last new germinants were observed in early September. The average germination pattern for these species was characterized by peaks in late May to early June and late July to early August (fig. 13). This generalized pattern is misleading, however. In reality, the two-peaked character is due to the occurrence of germination on about 50 percent of the plots during the first peak; the second peak resulted from germination which occurred on the latter plots plus those plots which had essentially no germination in May and June.

The germination pattern observed in this study was also reported for white spruce seed (natural seed fall) in Manitoba (Waldron 1966). This was not the most common pattern observed in Manitoba; Waldron reported that over a 4-year period, 67 and 27 percent of white spruce germination occurred in June and July, respectively. Waldron also noted that little germination was observed in May; in our study, the highest average number of white spruce germinants per plot was observed in late May. Horsley and Abbott (1970) observed that germination of spring-seeded birch was 70 to 80 percent complete within 4 weeks of artificial seeding.

In other field germination studies in Alaska, 85 percent of white spruce seedlings produced by naturally dispersed seeds and present at the end of the 1969 growing season had germinated prior to June 24 (Zasada and Gregory 1969), a result similar to the dominant pattern observed by Waldron (1966). Clautice[2/] reported that peak germination of spring-seeded spruce and birch occurred before the 1st week in July on north aspects. On south aspects, peak birch germination occurred earlier and spruce germination later relative to that on north aspects.

Germination patterns reflect temperature and moisture conditions. Although the water availability observations made in this study do not indicate the moisture stress conditions to which the seeds were exposed, they do provide the rainfall input and an approximation of seed bed dryness

---

[2/] Clautice, Stephen F. 1974. Spruce and birch germination on different seed beds and aspects in interior Alaska. 68 p. Master's Thesis, Univ. Alaska, Fairbanks.

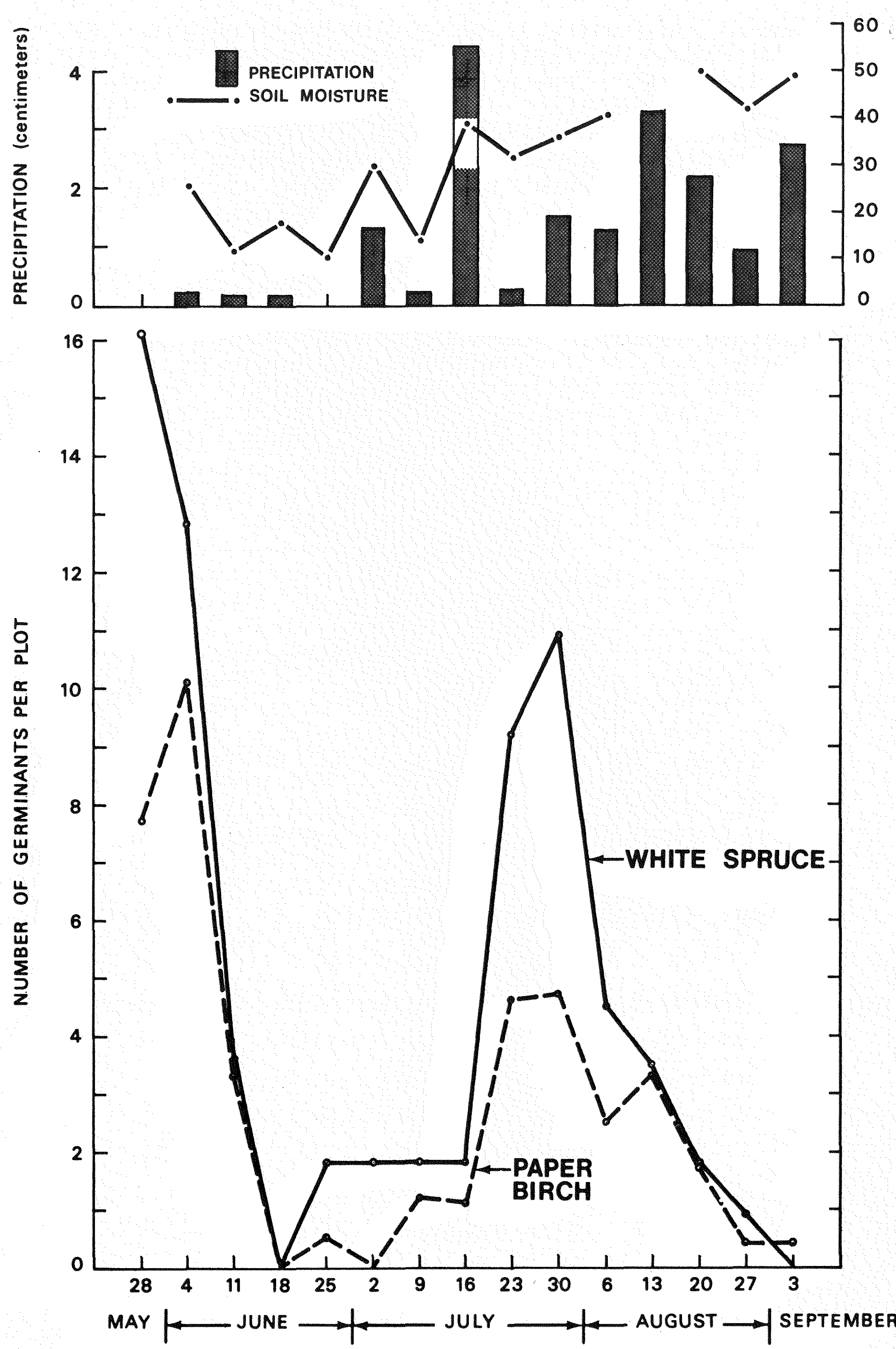


Figure 13.--Seasonal germination patterns of the 1970 white spruce and paper birch seed crops, precipitation, and soil moisture (volume basis, at 0-2 cm).

(fig. 13, table 12). The early germination was associated with high surface-soil moisture after snowmelt. The lull in activity was associated with a period of little rainfall when surface soil moisture was less than 20 percent. The July 2 moisture content was 30 percent, but this level was not maintained. In addition to lower average surface soil moisture, the water content in these layers was highly variable. Minimum moisture contents were from 3 to 4.5 percent. The second peak in germination occurred after relatively heavy rains preceding July 16. This and subsequent rain maintained average surface-soil moisture at 30 percent or greater. In addition, relative humidity was generally higher in July and August than in June (Barney and Berglund 1973).

Table 12--*Soil water content during the 1970 growing season*

Date	Depth (centimeters)						Precipitation
	0-2		3-5		6-8		
	$\overline{X}$	Range	$\overline{X}$	Range	$\overline{X}$	Range	
	Percent						Centimeters
June 4	26.1	4.4-37.9	24.5	13.8-36.0	31.1	19.4-38.9	0.02
June 11	12.3	3.0-18.8	25.0	14.1-34.3	24.1	17.0-30.2	.18
June 18	18.1	3.2-30.6	22.8	11.3-36.3	24.2	16.6-32.2	.18
June 25	10.5	3.3-23.8	20.3	10.6-31.2	22.6	18.7-24.8	0
July 2	29.7	27.2-33.9	30.4	29.2-31.5	30.4	23.8-36.1	1.27
July 9	14.2	10.1-20.6	23.9	16.4-30.9	26.5	17.8-23.4	.10
July 16	39.0	24.9-50.8	45.4	40.8-52.1	41.0	38.1-48.3	4.41
July 23	31.6	16.6-43.0	35.2	31.9-43.4	33.2	27.5-42.4	.22
July 30	36.3	29.5-44.1	39.0	35.0-44.9	38.0	28.0-50.8	1.49
Aug. 6	40.8	32.9-51.2	36.4	32.0-39.7	38.6	36.6-41.0	1.24
Aug. 13	--	--	--	--	--	--	3.30
Aug. 20	50.3	47.3-56.2	47.8	38.4-53.8	44.0	38.2-48.7	2.10
Aug. 27	41.8	35.3-45.3	40.2	34.7-47.2	38.8	35.4-42.4	.96
Sept. 3	48.9	39.0-56.3	37.8	40.0-51.1	38.9	35.2-44.6	2.77

Soil temperatures at the time germination began were 19° to 23°C (maximum) and 3° to 10°C (minimum). During the period when little or no rain fell and germination rate was low, surface temperatures as high as 40° to 50°C were observed. After early July when precipitation was occurring regularly, maximum surface temperature did not exceed 35°C and minimum surface temperatures were from 4° to 16°C.

The germination patterns for white spruce and birch were similar. Seeds germinating during the second peak are assumed to have been on the site during the first germination period. Their germination was prevented by adverse moisture or temperature conditions. The above assumption is based on the pattern of annual seed dispersal (fig. 11). That is, insignificant quantities of spruce and, it is assumed, birch seeds were dispersed in late June or July to account for the number of germinants which appeared during the second peak.

Survival and Population Dynamics

Survival during the first three growing seasons was assessed by subdividing the 1971 cohort (seedlings grown in the same year) into three subpopulations: those germinated prior to July 2 (May through June), July 3 to July 30 (July), and after July 30 (August). In both spruce and birch, summer survival was lowest for the May through June germinants. These seedlings were subjected to the most severe moisture and temperature conditions. Heaviest mortality for July and August spruce germinants and the June birch germinants occurred during the dormant season (table 13). At the end of the third growing season, the 1971 spruce cohort consisted of 60 percent May through June germinants, 32 percent July, and 8 percent August; the birch cohort consisted of 25, 47, and 28 percent June, July, and August germinants (table 14).

Table 13--*Percentage of white spruce and paper birch seedlings which survived the first summer and winter, by month of germination*

Seedlings	May-June		July		August	
	Summer survival[1]	Winter survival[2]	Summer survival	Winter survival	Summer survival	Winter survival
White spruce	53.8	48.0	83.2	20.1	71.2	15.9
Paper birch	49.2	41.7	73.2	58.8	65.0	57.0

[1] Percentage of all germinants for specified period.

[2] Percentage of seedlings surviving the first growing season.

Table 14--*Percentage of surviving 1971 white spruce and paper birch seedlings at the end of the first 3 growing seasons by month of germination*[1/]

Species	1971			1972			1973		
	May-June	July	August	May-June	July	August	May-June	July	August
White spruce	33.4	47.2	19.4	56.1	33.1	10.8	59.8	32.2	8.0
Paper birch	31.8	43.2	25.0	25.1	48.0	26.9	25.3	46.5	28.2

[1/] Percentage of seedlings alive at the end of each growing season.

White spruce and birch survival patterns differed during the 5-year period even though the percent survival was almost identical at the end of 5 years. This contrasts with the germination patterns mentioned earlier, which were similar. White spruce exhibited relatively little decline in density after the massive mortality of the first summer and winter. Birch survival, on the other hand, decreased relatively uniformly over the period (fig. 14, table 15).

Growth of the 1971 seedlings during their first growing season is shown in figure 15. Seedlings selected for each date represented the most vigorous individuals, and the sequence for both species best represents the shoot and root development of the earliest germinants. At any one time, seedlings representing all stages of development could be found. The July and August germinants are probably best represented by the germinants prior to those of July 2. Of particular interest is the relatively large size attained by dominant birch seedlings.

Place (1957), Waldron (1966), and Ronco (1967) reported, as observed in this study, differential winter mortality of conifer seedlings related to the time during which germination occurred (table 13); that is, spruce seedlings which germinated in July and August suffered more overwinter mortality than those germinating earlier. Birch exhibited a different pattern in that July and August germinants survived the winter better than those from June. In a study conducted in the subalpine forests of Alberta, Ackerman (1957) reported that survival in two artificial seeding experiments (fall seeded) was 76 and 35 percent at the end of the second growing season. Horsley and Abbott (1970) reported that 1st-year summer survival for paper birch ranged from 54 to 86 percent, winter survival from 31 to 56 percent, and survival at the end of the second growing season was from 24 to 47 percent.

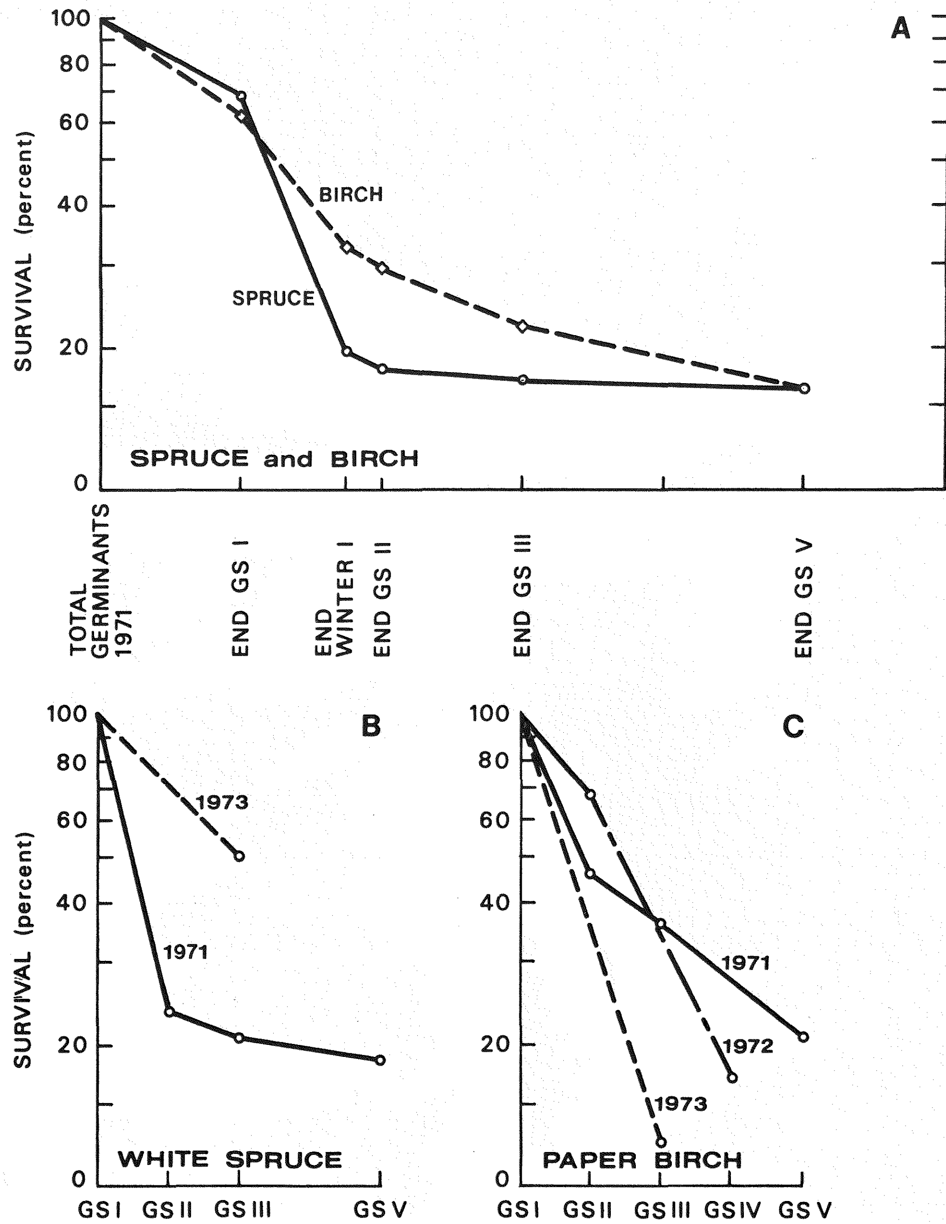


Figure 14.--Survival of white spruce and paper birch seedlings over five growing seasons (1971-75): A, 1971 spruce and birch germinants; B, 1971 and 1973 spruce germinants; C, 1971, 1972, and 1973 birch germinants. GS = growing season.

Table 15--*White spruce and paper birch seedling population composition by year of germination*

Item	1971	1972			1973				1975				
	Year of germination	Year of germination			Year of germination				Year of germination				
	1971	1971	1972	Total	1971	1972	1973	Total	1971	1972	1973	1974 and 1975	Total
	Number of seedlings per plot[1]												
White spruce	48.6	11.4	--	11.4	10.0	--	9.7	19.7	9.0	--	4.9	0	13.9
Standard error	20.7	8.8	--	8.8	7.8	--	8.3	9.6	6.8	--	4.9	--	7.5
Frequency[2]	100	95	--	95	95	--	90	100	95	--	80	--	100
Paper birch	25.6	11.8	3.6	15.4	9.2	2.4	4.3	15.9	5.3	.5	.2	0	6.0
Standard error	16.8	12.2	2.8	12.9	9.2	2.1	3.9	10.3	6.6	.9	.4	--	6.3
Frequency	95	85	75	90	85	75	80	95	80	30	20	--	90

1/ For conversion to density per square meter, multiply spruce by 3.5 and birch by 31.8.

2/ Frequency on germination plots. Frequency on square-meter vegetation plots, 100 percent for both species.

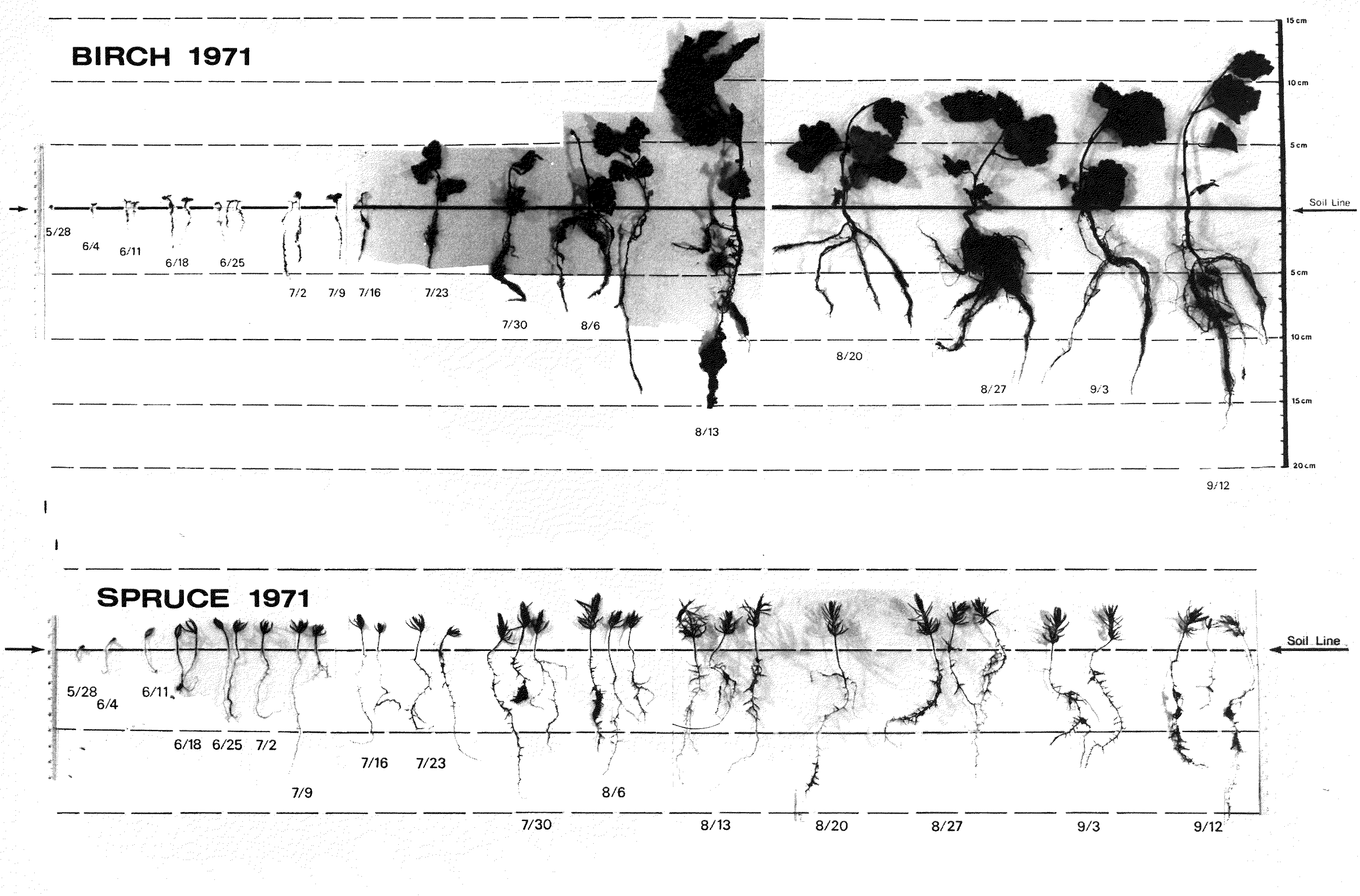


Figure 15.--Development of white spruce and paper birch seedlings as indicated by weekly excavation of vigorous seedlings.

Germinants were added to the spruce population in 1973 and to the birch population in 1972 and 1973 (table 15). The 1973 germinants were the result of heavy seed fall by both species in 1972 (spruce, 531 filled seeds per square meter (table 16); birch, 1,800 per square meter). By the end of the 1975 growing season, these seedlings contributed 35 percent to the spruce population and 12 percent to the birch population (a comparably poor contribution).

Table 16--*White spruce seed fall in a forest opening in interior Alaska for seed years 1970-74*

Year	Total seed per square meter	Filled seed per square meter
1970	960 ± 26[1/]	666 ± 20
1971	44 ± 5	18 ± 5
1972	996 ± 76	531 ± 38
1973	68.0 ± 11	20 ± 8
1974	0	0

1/ Standard deviation.

The dominant seedlings in the study area, however, were those produced by the 1970 seed crop. Dominant spruce seedlings of 1971 origin averaged 18.5 cm tall while those produced in 1973 were 5 cm; the birch produced in 1971 were 29.4 cm tall at the end of 1975. Barring natural disaster, it appears that the seedlings from the 1970 seed crop will continue to dominate the area.

Seed crop efficiency can be measured by seedling:seed ratios. The following tabulation compares the estimates for white spruce from this study with those reported by Ackerman (1957).

Year of germination	Growing season: First	Third	Fifth
	(Number of seedlings:number of seeds)		
1971 (present study)	1:4	1:18	1:21
1973 (present study)	1:16	1:31	--
Experiment 1 (Ackerman 1957)	1:7	1:11	1:13
Experiment 2 (Ackerman 1957)	1:13	1:42	1:67

The 1971 values and Ackerman's values are for mineral soil seed beds where all vegetation was removed, conditions reported to be the most desirable for germination and initial establishment (Dobbs 1972). The other extreme is represented by seed beds consisting of organic matter of varying depths. Under these conditions Ackerman (1957) reported ratios of one seedling per 228 seeds and Eis (1967b) 1:200 seeds. In interior Alaska where organic and moss layers tend to be thicker, these ratios are probably higher. Comparative values for the 1972 birch seed crop were 1:450 and 1:9,000 after one and three growing seasons.

Seedling production by two essentially identical seed crops (table 16), relative seedling size, poorer performance by birch seedlings produced by the 1971 and 1972 seed crops, and the associated changes in soil surface conditions and plant cover provide insight into the question of the deterioration of seed bed conditions and an environment suitable to seedling survival. Site preparation created large areas of mineral soil for the 1970 seed crop. By 1972, however, the area covered by mineral soil had decreased to 19 percent even though frequency of occurrence was 100 percent; in 1975, exposed mineral soil was 3 percent and frequency 67 percent (table 17).

The primary reasons for the decline in the area of exposed mineral soil were increased plant litter and moss cover (table 17). The effect of moss cover on seedling establishment goes beyond the influence its growth has on the area of exposed mineral soil. By 1975, the height of the moss was equal to that of the 1973 seedlings and was in a position to compete with seedlings for moisture, light, and nutrients. These data suggest that seed beds remain receptive for 3 to 5 years for spruce and for a shorter time for birch under the study conditions. These results for spruce agree in general with those from central British Columbia (Arlidge 1967).

Woody and herbaceous plant cover changed significantly between 1971 and 1973 (table 17). These changes were the reason for the annual increases in area covered by plant litter; they created a different light, chemical, and moisture environment within the soil and air layers most important to germination and seedling survival. By the end of the 1973 growing season, plant cover on the meter-square plots averaged 90 percent. Birch and horsetail (*Equisetum arvense* L.) were the dominant species in terms of cover. In addition to the potential competitive and inhibitive (allelopathic) effects of this vegetation, there is also the possibility of physical damage to seedlings resulting from litter fall. Gregory (1966)

Table 17--Changes in seed bed conditions and frequency and percent cover of vascular and nonvascular plants, litter, and exposed mineral soil in a forest opening in interior Alaska

(In percent)

Seed bed conditions and plants	1971 (May)	1971 (Sept.)	1972	1973	1975
	SEED BED CONDITIONS				
Mineral soil:					
Frequency	100	100	100	83	67
Cover	85	72	19	14	3
Leaf litter:					
Frequency	100	100	100	100	100
Cover	7	8	10	24	89
Other litter:					
Frequency	--	42	92	100	17
Cover	--	2	2	2	1
	NONVASCULAR PLANTS				
Liverworts:					
Marchantia polymorpha--					
Frequency	--	25	8	33	8
Cover	--	1	1	1	3
Mosses:					
Ceratodon purpurea--					
Frequency	--	--	--	100	75
Cover	--	--	--	65	6
Polytrichum spp.--					
Frequency	--	--	--	92	100
Cover	--	--	--	18	25
Other mosses--					
Frequency	8	83	50	90	50
Cover	1	28	21	1	1
	VASCULAR PLANTS				
Herbs:					
Epilobium angustifolium--					
Frequency	25	75	75	100	100
Cover	1	8	11	9	6
Calamagrostis canadensis--					
Frequency	8	50	58	67	75
Cover	1	3	10	13	22
Equisetum arvense--					
Frequency	--	100	100	100	100
Cover	--	6	25	24	22
Geranium Bicknellii--					
Frequency	--	92	92	92	75
Cover	--	8	14	2	1
Corydalis aurea--					
Frequency	--	75	42	8	--
Cover	--	5	1	1	--
Moehringia lateriflora--					
Frequency	--	8	17	8	33
Cover	--	1	1	1	1
Mertensia paniculata--					
Frequency	--	8	17	8	8
Cover	--	1	1	1	1
Agrostis scabra--					
Frequency	--	8	8	50	42
Cover	--	1	1	1	2
Galium boreale--					
Frequency	--	8	8	8	8
Cover	--	1	1	1	1
Solidago or *Erigeron*--					
Frequency	--	8	--	8	17
Cover	--	1	--	1	1
Taraxacum spp.--					
Frequency	--	--	8	8	8
Cover	--	--	1	1	1
Low shrubs:					
Vaccinium vitis-ideae--					
Frequency	--	--	--	--	8
Cover	--	--	--	--	1
Tall shrubs:					
Viburnum edule--					
Frequency	--	17	8	8	8
Cover	--	1	1	1	1
Ribes triste--					
Frequency	--	50	67	92	83
Cover	--	3	3	3	2
Rosa acicularis--					
Frequency	--	17	33	33	33
Cover	--	1	1	1	1
Salix spp.--					
Frequency	--	--	50	75	42
Cover	--	--	1	1	1
Salix arbusculoides--					
Frequency	--	--	--	50	33
Cover	--	--	--	1	2
Salix alaxensis--					
Frequency	--	--	--	42	42
Cover	--	--	--	1	1
Alnus crispa--					
Frequency	--	--	--	8	17
Cover	--	--	--	1	1
Betula papyrifera--					
Frequency	--	100	100	100	100
Cover	--	9	23	32	37
Picea glauca--					
Frequency	--	100	100	100	100
Cover	--	1	2	2	11
Populus tremuloides--					
Frequency	--	--	25	50	42
Cover	--	--	1	1	1
Populus balsamifera--					
Frequency	--	--	17	25	25
Cover	--	--	1	1	1

reported that white spruce seedlings less than 4 years old could be damaged or smothered by leaf fall in an 80-year-old birch stand. The nature of the litter produced by the herbaceous and woody vegetation on this site is significantly different from that in an 80-year-old birch stand, but the litter could have damaged spruce and birch seedlings which germinated in 1973.

The dominant vascular plants which regenerated in abundance, in addition to spruce and birch, were fireweed (*Epilobium angustifolium* L.), horsetail, and bluejoint (*Calamagrostis canadensis* (Michx.) Beauv.). These species are all common in undisturbed white spruce stands. Two species, *Geranium Bicknellii* Britt. and *Corydalis aurea* Willd., which were not found in the undisturbed white spruce stands, were important during the first two growing seasons after clearing. By the end of the fifth growing season, *Corydalis* was no longer present on the plots. *Geranium* was still present; however, its frequency of occurrence had declined from 92 to 75 percent and its percent cover had decreased from 14 percent (second growing season) to less than 1 percent. Tall shrubs had low percent cover; but the willows (*Salix* spp.), as a group, and American red currant (*Ribes triste* Pall.) had relatively high frequencies of occurrence (table 17).

Management Implications

We feel that the observations reported here have demonstrated several potentially important things to land managers interested in obtaining natural regeneration of white spruce. These are:

1. White spruce stands in three areas of Alaska produced large cone and seed crops. This indicates that the basic seed input is periodically available over much of this species' range in the State.

2. Weather conditions can prevent the maturity of seed crops. In 1970, immaturity occurred in stands above 600 m and north of the Arctic Circle. These observations indicate that if seed collection from a given area is necessary, seed development should be monitored closely to determine the right time to collect cones. The best method of handling cones should be used to insure that seed of the highest possible quality is secured.

3. Seed disperal began in early September. Thus, site preparation should be accomplished earlier to get maximum benefit from a particular seed crop.

4. Abundant white spruce (and paper birch) natural regeneration can be obtained on upland sites in the Tanana Valley during an excellent seed year. The receptivity of the seed bed is significantly decreased by the third growing season, making adequate germination and seedling survival increasingly difficult to obtain. When possible, site preparation should coincide with an adequate seed year.

It must be stressed that the general applicability of the results of this study must be tested over a period of years and different soil and site conditions. The main importance of the observations is that they indicate, in general, white spruce natural regeneration follows similar patterns to those observed elsewhere. An important departure from the generalized North American regeneration considerations, but not from those of northern Finland, Sweden, and Norway, is the limitation on natural regeneration which may occur in some years as a result of immature seed crops.

Summary

The 1970 cone and seed crop for white spruce was the best crop recorded since 1958. Climatic conditions considered favorable for formation of reproductive buds occurred in 1969, resulting in a large number of male and female flowers in the spring of 1970. This paper reports on male strobili development and pollen dispersal, cone development, seed maturation and dispersal, and the germination of seed and survival of the seedlings produced by this seed crop.

1. In 1970, flowering in white spruce was found to be strongly influenced by elevation. Flowering at low elevation (135 m) occurred from May 25 to 27; at higher elevations (600 m or higher), flowering was 3 to 5 weeks later.
2. Cone size was significantly influenced by seed source. In the Fairbanks area cone expansion was completed by July 1. Dry weight continued to increase until mid-July. Percent moisture content decreased sharply from early July to mid-July, decreased gradually from mid-July to mid-August, and decreased more rapidly from mid-August until seed dispersal began.
3. At lower elevations, seed maturity increased steadily from early July to early August. Poor seed development (immature embryos) was observed in stands above 600 m and north of the Arctic Circle.
4. Seed dispersal in the Fairbanks area began 99 days after pollination. Total seed fall in undisturbed white spruce stands varied from 250 to 2,000 seeds per square meter (1 to 8 million per acre). Percent filled seed was 38 to 77 percent.
5. Seed germination began in late May and was characterized by peaks in late May and early June and late July and early August. This seasonal pattern was associated with summer moisture availability.
6. White spruce seedlings which germinated in May and June 1971 had the highest survival over a 3-year period. The greatest mortality occurred in the summer and winter after germination.

7. At the end of 5 years, the white spruce seedlings produced by the 1970 seed crop comprised 65 percent of the spruce seedlings in the study area and the dominants produced by this seed crop were at least two to three times larger than those produced by the 1973 seed crop.

8. Seed bed and seedling survival conditions had deteriorated significantly by the end of the third growing season.

9. Observations made of paper birch germination and survival indicated that the germination pattern for birch was similar to that of spruce. Survival differed in that birch seedling density decreased more gradually over the 5-year observation period than did spruce seedling density.

Literature Cited

Ackerman, R. F.
1957. The effect of various seedbed treatments on the germination and survival of white spruce and lodgepole pine seedlings. Can. Dep. North. Aff. and Nat. Resour. For. Branch, For. Res. Div. Tech. Note No. 63, 23 p.

Andersson, E.
1965. Cone and seed studies in Norway spruce (*Picea abies* (L.) Karst.) Stud. For Suec. NR 23, 214 p.

Arlidge, J. W. C.
1967. The durability of scarified seedbeds for spruce regeneration. B. C. For. Serv. Res. Note No. 42, 20 p.

Barney, Richard J., and Erwin R. Berglund.
1973. Summary of climatic data for the Bonanza Creek Experimental Forest, interior Alaska. USDA For. Serv. Res. Note PNW-201, 43 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Bingham, R. T., K. C. Wise, and S. P. Wells.
1969. Aberrant cones in western white pine. USDA For. Serv. Res. Note INT-86, 4 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Chalupka, W., and M. Giertych.
1973. Seed years in *Picea abies* (L.) Karst. Arbor. Kornickie 18:183-186.

Clausen, J. J., and T. T. Kozlowski.
1965. Seasonal changes in moisture content of gymnosperm cones. Nature 206(4979):112-113.

Cram, W. H., and H. A. Worden.
1957. Maturity of white spruce cones and seeds. For. Sci. 3(3):263-269.

Crossley, D. I.
1953. Seed maturity in white spruce. Can. Dep. Resour. and Dev. Res. Note 102, 18 p.

Dobbs, R. C.
1972. Regeneration of white spruce and Engelmann spruce. A literature review with special reference to the British Columbia interior. Can. Dep. Environ. Can. For. Serv. Inf. Rep. BS-X-69, 77 p.

Edwards, D. G. W.
1971. An abberant cone in western hemlock. Can. For. Serv. Bimon. Res. Notes 27, p. 33.

Eis, S.
1967a. Cone crops of white and black spurce are predictable. For. Chron. 43(3):247-252.

Eis, S.
1967b. Establishment and early development of white spruce in the interior of British Columbia. For. Chron. 43(2): 174-177.

Fechner, G. H.
1974. Maturation of blue spruce cones. For. Sci. 20(1): 47-50.

Fraser, D. A.
1958. The relation of environmental factors to flowering in spruce. *In* The physiology of forest trees, p. 629-642. K. V. Thimann, ed. The Ronald Press, New York.

Funsch, R.
1964. A summary of seasonal temperature and precipitation data for the interior forest area of Alaska. USDA For. Serv. Res. Note NOR-9, 50 p. North. For. Exp. Stn., Juneau, Alaska.

Gregory, R. A.
1966. The effect of leaf litter upon establishment of white spruce beneath paper birch. For. Chron. 43(3): 251-255.

Gustafsson, A., and M. Simak.
1958. X-ray diagnostics and seed quality in forestry. Int. Union For. Res. Organ. 12th Congr. Proc. Publ. No. 56/22/102 Sect. 22, 12 p. [Oxford, England.]

Hellum, A. K.
1969. Variation in cotyledon number and seed weight in white spruce in Alberta. Proc. 11th Meet. Comm. For. Tree Breed. Can., Aug. 1968, p. 65-76. Macdonald College.

Horsley, S. B., and H. G. Abbott.
1970. Direct seeding of paper birch in strip clearcutting. J. For. 68(10):635-638.

International Seed Testing Association (ISTA)
1966. International rules for seed testing. Int. Seed Test. Assoc. Proc. 31(1):1-152.

Machaníček, Jiri.
1973. Economic collection of cones of forest conifers on the basis of preceding estimation of cone crop. Int. Symp. Seed Process. Vol. 1, Pap. No. 12, 22 p.

Matthews, J. D.
1963. Factors affecting the production of seed by forest trees. For. Abstr. 24(1):I-X.

Nelson, D. L., and R. G. Krebill.
1970. Effect of *Chrysomyxa pirolata* cone rust on dispersal and viability of *Picea pungens* seeds. Phytopathology 60(9):1305.

Nienstaedt, H., and A. Teich.
1972. The genetics of white spruce. USDA For. Serv. Res. Pap. WO-15, 24 p. Washington, D.C.

Norin, B. N.
1958. Germinative and vegetative reproduction of trees in wooded tundra. Rastitel'nost'Krainego Severa SSSR 3:154-244. [Translated from Russ. Israel Program Sci. Transl., 1965. IPST Cat. No. 1309.]

Place, I. C. M.
1957. The influence of seedbed conditions on the regeneration of spruce and balsam fir. Can. Dep. North. Aff. and Nat. Resour. For. Bull. 117, 87 p.

Powell, G. R.
1975. Seedfall in red spruce. For. Chron. 51(2):55-58.

Rauter, R. M., and J. L. Farrar.
1969. Embryology of *Picea glauca* (Moench) Voss. 16th Northeast. For. Tree Improv. Conf. Proc., p. 13-24.

Ronco, Frank.
1967. Lessons from artificial regeneration studies in a cutover beetle-killed spruce stand in western Colorado. USDA For. Serv. Res. Note RM-90, 8 p. Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo.

Safford, L. O.
1974. *Picea* A. Dietr. spruce. *In* Seeds of woody plants in the United States. U.S. Dep. Agric., Agric. Handb. No. 450, p. 587-597.

Sarvas, R.
1957. Studies on the seed setting of Norway spruce. Det. Nor. Skogforsøksvesen 14:534-556.

Sarvas, R.
1968. Investigations on the flowering and seed crop of *Picea abies*. [Proc. Finn. For. Res. Inst.] Metsantutkimuslaitoksen Julkaisuja 67.5, 84 p.

Simak, M.
1957. The X-ray contrast method for seed testing. Medd. Från Statens Skogsforskningsinst. Band 47 NR4, 22 p.

Teich, A. H.
1970. Genetic control of female flower color and random mating in white spruce. Can. Dep. Fish. and For. Bimon. Res. Notes 26, p. 2.

Waldron, R. M.
1965. Cone production and seedfall in a mature white spruce stand. For. Chron. 41(3):314-329.

Waldron, R. M.
1966. Factors affecting natural white spruce regeneration on prepared seedbeds at the Riding Mountain Experimental Area, Manitoba. Can. Dep. For. and Rural Dev. For. Branch Publ. No. 1169, 41 p.

Wang, B. S. P.
1974. Testing and treatment of Canadian white spruce seed to overcome dormancy. Proc. Assoc. Off. Seed Anal. 64:72-79.

Werner, R. A.
1964. White spruce seed loss caused by insects in interior Alaska. Can. Entomol. 96(11):1462-1464.

Winton, L. L.
1964. Meiosis and pollen release in white spruce and black spruce and their hybrid. Minn. For. Note 154, 2 p.

Zasada, John C.
1971. Frost damage to white spruce cones in interior Alaska. USDA For. Serv. Res. Note PNW-149, 7 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Zasada, John C.
1973. Effect of cone storage method and collection date on Alaskan white spruce (*Picea glauca*) seed quality. Int. Symp. Seed Process. Vol. 1, Pap. No. 19, 10 p.

Zasada, John C., and Robert A. Gregory.
1969. Regeneration of white spruce with reference to interior Alaska: a literature review. USDA For. Serv. Res. Pap. PNW-79, 37 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Zasada, John C., and Robert A. Gregory.
1972. Paper birch seed production in the Tanana Valley, Alaska. USDA For. Serv. Res. Note PNW-177, 7 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Zasada, John C., and Leslie A. Viereck.
1970. White spruce cone and seed production in interior Alaska 1957-68. USDA For. Serv. Res. Note PNW-129, 11 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Ziller, W. G.
1974. The tree rusts of western Canada. Can. For. Serv. Publ. No. 1329, 272 p.

GPO 986-380

Sarvas, R.
1968. Investigations on the flowering and seed crop of *Picea abies*. [Proc. Finn. For. Res. Inst.] Metsantutkimuslaitoksen Julkaisuja 67.5, 84 p.

Simak, M.
1957. The X-ray contrast method for seed testing. Medd. Från Statens Skogsforskningsinst. Band 47 NR4, 22 p.

Teich, A. H.
1970. Genetic control of female flower color and random mating in white spruce. Can. Dep. Fish. and For. Bimon. Res. Notes 26, p. 2.

Waldron, R. M.
1965. Cone production and seedfall in a mature white spruce stand. For. Chron. 41(3):314-329.

Waldron, R. M.
1966. Factors affecting natural white spruce regeneration on prepared seedbeds at the Riding Mountain Experimental Area, Manitoba. Can. Dep. For. and Rural Dev. For. Branch Publ. No. 1169, 41 p.

Wang, B. S. P.
1974. Testing and treatment of Canadian white spruce seed to overcome dormancy. Proc. Assoc. Off. Seed Anal. 64:72-79.

Werner, R. A.
1964. White spruce seed loss caused by insects in interior Alaska. Can. Entomol. 96(11):1462-1464.

Winton, L. L.
1964. Meiosis and pollen release in white spruce and black spruce and their hybrid. Minn. For. Note 154, 2 p.

Zasada, John C.
1971. Frost damage to white spruce cones in interior Alaska. USDA For. Serv. Res. Note PNW-149, 7 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Zasada, John C.
1973. Effect of cone storage method and collection date on Alaskan white spruce (*Picea glauca*) seed quality. Int. Symp. Seed Process. Vol. 1, Pap. No. 19, 10 p.

Zasada, John C., and Robert A. Gregory.
1969. Regeneration of white spruce with reference to interior Alaska: a literature review. USDA For. Serv. Res. Pap. PNW-79, 37 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Zasada, John C., and Robert A. Gregory.
1972. Paper birch seed production in the Tanana Valley, Alaska. USDA For. Serv. Res. Note PNW-177, 7 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Zasada, John C., and Leslie A. Viereck.
1970. White spruce cone and seed production in interior Alaska 1957-68. USDA For. Serv. Res. Note PNW-129, 11 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Ziller, W. G.
1974. The tree rusts of western Canada. Can. For. Serv. Publ. No. 1329, 272 p.

The mission of the PACIFIC NORTHWEST FOREST AND RANGE EXPERIMENT STATION is to provide the knowledge, technology, and alternatives for present and future protection, management, and use of forest, range, and related environments.

Within this overall mission, the Station conducts and stimulates research to facilitate and to accelerate progress toward the following goals:

1. Providing safe and efficient technology for inventory, protection, and use of resources.
2. Developing and evaluating alternative methods and levels of resource management.
3. Achieving optimum sustained resource productivity consistent with maintaining a high quality forest environment.

The area of research encompasses Oregon, Washington, Alaska, and, in some cases, California, Hawaii, the Western States, and the Nation. Results of the research are made available promptly. Project headquarters are at:

Fairbanks, Alaska	Portland, Oregon
Juneau, Alaska	Olympia, Washington
Bend, Oregon	Seattle, Washington
Corvallis, Oregon	Wenatchee, Washington
La Grande, Oregon	

Mailing address: Pacific Northwest Forest and Range Experiment Station
P.O. Box 3141
Portland, Oregon 97208